

Analysis of acoustic elements and syntax in communication sounds emitted by mustached bats

Jagmeet S. Kanwal, Sumiko Matsumura,^{a)} Kevin Ohlemiller, and Nobuo Suga
Department of Biology, Washington University, St. Louis, Missouri 63130

(Received 22 November 1993; accepted for publication 30 April 1994)

Mustached bats, *Pteronotus parnellii parnellii* spend most of their lives in the dark and use their auditory system for acoustic communication as well as echolocation. The sound spectrograms of their communication sounds or "calls" revealed that this species produces a rich variety of calls. These calls consist of one or more of the 33 different types of discrete sounds or "syllables" that are emitted singly and/or in combination. These syllables can be further classified as 19 simple syllables, 14 composites, and three subsyllables. Simple syllables consist of characteristic geometric patterns of CF (constant frequency), FM (frequency modulation), and NB (noise burst) sounds that are defined quantitatively using statistical criteria. Composites consist of simple syllables or subsyllables conjoined without any silent interval. Most syllable types exhibit a large intrinsic variation in their physical structure compared to the stereotypic echolocation pulses. Syllable domains are defined on the basis of multiple parameters, although these can be collapsed onto three dimensions that capture 99% of the measured variation among different types of syllables. Temporal analysis of multisyllabic constructs reveals several syntactical rules for syllable transitions.

PACS numbers: 43.80.Ka, 43.80.Jz

INTRODUCTION

For many species of microchiropteran bats that spend much of their life in the darkness of caves, sound is not only critical for echolocation but also for acoustic communication with distantly located conspecifics (Gould, 1977). Studies on acoustic communication in microchiropteran bats, e.g., *Myotis lucifugus* (Gould, 1971; Fenton, 1977), *Antrozous pallidus* (Brown 1976), *Noctilio albiventris* (Brown *et al.*, 1983), *Carollia perspicillata* (Porter, 1979), *Rhinolophus ferrumequinum* (Matsumura, 1979, 1981), and *Tadarida brasiliensis* (Balcombe, 1990) clearly show that bats, like many other mammals, rely heavily on acoustic signals for social interactions. Behavioral studies also indicate the existence of a complex social structure and strong group bonds in many species of bats (Bradbury, 1977; Fenton, 1985). Despite the rich knowledge of various sound patterns and their associated behaviors in bats, there have been no quantitative treatments of the common acoustic patterns in their sounds. Such information may greatly facilitate our understanding of the construction and usage of complex communication sounds. In fact, knowledge of the natural variation in the different sound patterns is critical for any kind of rigorous study showing the association of particular sound patterns with specific behavioral repertoires. Thus it is known that in non-human primates one variant of a sound pattern is rarely used in more than two different social situations (Gautier, 1974; Green, 1975; Pola and Snowdon, 1975; Eisenberg, 1976; Snowdon, 1982).

Knowing the natural range of variation of different types of communication sounds is also useful for generating natural and synthetic variants as stimuli for studying the neural

processing of communication sounds. This aspect of the study of communication sounds has been investigated only in a few nonmammalian species, e.g., the white-crowned sparrow (Margoliash, 1983), zebra finch (Margoliash and Fortune, 1992), and the leopard frog (Fuzessery and Feng, 1983), and a single mammalian species, namely, the squirrel monkey (Wollberg and Newman, 1972; Winter and Funkenstein, 1973; Newman and Wollberg, 1973a,b; Newman, 1979). Other mammalian species, e.g., the humpback whale (Payne and McVay, 1971), bottlenose dolphin (Sales and Pye, 1974), mouse (Ehret, 1989), and several primate species (Sutton, 1979; Snowdon *et al.*, 1982), in which extensive field work and acoustic analysis of communication sounds has been performed, are either unsuitable or have been generally neglected with respect to in-depth studies of the neural processing of communication sounds. Alternatively, in those species in which the neurobiology of the auditory system is relatively well studied, e.g., the mouse, chinchilla, gerbil, or cat, the behavioral and neurophysiological aspects of acoustic communication have not been addressed.

Our aim was to analyze the structure of communication sounds (hereafter, "calls") of the mustached bat for extensive neurophysiological studies of call processing. Our study also constitutes a first step toward future behavioral studies of acoustic communication as well as investigations of the mechanisms of vocalization and perception of calls in this species. We chose the mustached bat, *Pteronotus parnellii parnellii*, because its auditory system is the best understood neurophysiologically among mammals (see reviews by Suga, 1984, 1990; Pollak and Cassedy, 1989). We performed a statistical analysis of the physical structure of calls and also developed a classification scheme. We categorized the calls according to this scheme, quantified variations in their spectral components and described the temporal patterns of asso-

^{a)}Current address: School of Allied Health Sciences, Yamaguchi University, Ube, 755 Japan.

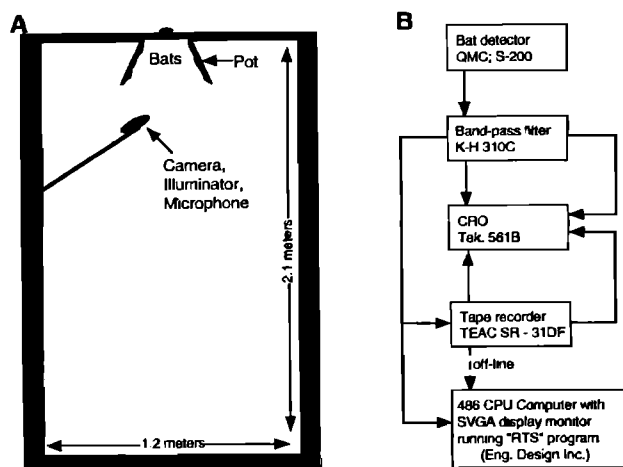


FIG. 1. (a) Schematic of the setup for recording vocalizations from bats flying and roosting in a colony in the flight room. (b) Flow chart of equipment and methodology used for recording calls of bats.

ciation or "syntax" (see Snowden, 1982; Marler and Peters, 1989) of a variety of acoustic elements.

I. MATERIALS AND METHODS

A. Acquisition and maintenance of bats

Sixty-five (41 males and 24 females) adult mustached bats, *Pteronotus parnellii parnellii*, were collected from Windsor Cave located in Jamaica and kept in a flight room (1.2 m×2.1 m×4.6 m). Two inverted clay flower pots coated with cement and fixed on the roof of a flight room served as roosting sites for the bats. The flight room was maintained at a relative humidity level of 55% and a temperature of 28 ° to 30 °C. The bats hung on the inner surface of the pots most of the time and fed on meal worms and drank water from trays placed at the corners of the room.

B. Recording and analysis of calls

After about one month of captivity, i.e., after the bats became accustomed to the new environment and food, the calls of mustached bats were recorded over a six month period [Fig. 1(a)]. Recordings of calls were obtained from two populations of bats acquired annually from the same cave over two consecutive years. A broadband microphone (QMC; S-200), a bandpass filter (2–100 kHz), and a tape recorder (TEAC SR-31DF or RACAL ST0705) with a flat frequency response between 2 and 100 kHz were used for recording the calls [Fig. 1(b)]. To minimize the effect of head aim on variations in the recorded signals, the microphone was positioned approximately 60 cm from the center of the pot and directed toward the center of the bat colony. The sensitivity of the recording apparatus was optimized for recording single calls of roosting bats. An infrared video camera and an industrial grade video recorder were used for monitoring the physical condition of the bats and for future correlation of behaviors with call types. Variability in the calls recorded from flying bats was controlled by restricting the recording periods to short times when flying activity was minimal, as observed on the video monitor. However, to

TABLE I. Mean values of acoustic parameters for "constant frequency (CF) type" of syllables.

Parameter	TCFs	QCFL	sQCF	tQCF
Overall syllable duration (ms)	38.38	302.43	11.10	14.11
Frequency of fundamental (f_0) in kHz	30.39	7.92	8.61	8.94
Peak frequency of fundamental (kHz)	30.39	8.20	8.61	8.94
Frequency of predominant harmonic (kHz)	60.78	7.92	8.61	8.94
% frequency modulation in harmonics	2.13	3.60	0.00	18.04
Max. depth of freq. modulation for f_0 (kHz)	0.65	0.28	0.00	3.20
Rate of frequency modulation (max. kHz/ms)	0.01	0.00	0.00	1.01

identify calls that might be produced during flight, separate recordings were also obtained during those times of the day, e.g., late evening, when flying activity was maximal. Audio and video recorders were synchronized to enable accurate cross reference of the two inputs by digital meters of both machines.

Since the spectra of many calls from different bats were cluttered with a continuous stream of orientation sounds (echolocation pulses), we also recorded the calls from an isolated group of two or three bats placed in an echo-attenuated cage. Combinations of bats in these groups included two males, one male and one female, and two males and one female. Calls were not emitted by single isolated bats, although these bats emitted echolocation pulses.

The recorded calls were digitized and analyzed using the RTS™ and SIGNAL™ programs (Engineering Design Inc.) running on an 80486 CPU (Intel Corp.). The tape recorded calls were first scanned by playing back at one fourth of the original speed into an audio monitor and into the computer so that RTS generated running spectrograms of these sounds. This allowed simultaneous audio and visual inspection of the calls. The sampling rate of the A/D board was 250 kHz. This enabled storage of up to a 1.1-s-long signal on the display screen and in the random access memory of the computer for on-line analysis. The frequency and time windows were adjusted to optimize the identification of the fundamental frequency and harmonics in the calls. Further analysis was performed by slowed down playback of calls for making measurements (see Table I) from the screen with a cross-hairs cursor. A hard copy of the screen display was obtained using a 300-dpi laser printer and the digitized wave form was also stored as a SIGNAL file for archiving. Finally, representative examples of calls and call segments were played back at normal speed and digitized using SIGNAL.

C. Classification and statistical analyses of syllables

Our classification scheme for calls was based on quantitative descriptions of the sound spectrograms. Our analyses were neither constrained nor influenced by the observable behaviors. The richness of the overall repertoire of calls is difficult to assess by observation of the emitter in a specific behavioral context. However, a large sample of the calls obtained at different times from a colony of animals in a semi-natural environment can be used to identify the structural elements (syllables) and their combinations. Values of individual parameters characterizing syllables within calls were entered into a database and the classification of syllables was

statistically tested and modified on the basis of these results. The frequency distributions of different parameters obtained from a sample of 20 to 30 examples of each syllable type were tested for normality. At least six examples were analyzed for syllable types that were uncommon. Bimodally distributed parameters, such as the duration of a constant frequency (CF), the rate of downward sweep of a frequency modulated (FM), and the rate of oscillation of a sinusoidal FM (SFM) sound, were analyzed and used to identify simple syllables within composites. The final classification scheme was analyzed further using multivariate analysis procedures to test for the "goodness of fit" and to define the parametric boundaries (decision domains) of the syllable types represented by the multiple dimensions (up to 14).

Discriminant analysis was used to test for goodness of fit between the given classification scheme and the grouping of syllables as predicted by the model. Discriminant analysis assumes that the distribution of the measured parameters is known, that the data fit a multivariate model and tests the multivariate general linear hypothesis for a given set of variables and predefined groups using a multiple analysis of variance (MANOVA) procedure (Hand, 1981; McLachlan, 1992). This procedure generates probability density functions for the various parameters in each group which are used to calculate the probability of misclassification and the predicted group (type) of each syllable used in the quantification procedure. We, therefore, first plotted the distributions of the various parameters characterizing the sound spectrograms. If the chosen parameters showed a close fit to either a normal or a half-normal frequency distribution, their values were included in a database that was used to perform discriminant analysis with "syllable type" as the significant factor accounting for most of the variation.

Discriminant analysis was used to generate quantitative rules, which were used for assigning a syllable to an old or a new group. The strategy of stepwise backward elimination was used to arrive at the "best-fitting" model. After pooling all the measured variables, poor predictors were removed from the model and good predictors allowed to reenter the model until a given subset of variables provided the best fit. The test procedure generated a matrix of the syllables in which rows represented the predefined groups and columns represented the predicted groups. The final results of this tabulation showed an excellent fit for most of the predefined syllable types.

We employed the principal components model of factor analysis to view the internal relationship between the different parameters of syllables. The goal of principal components analysis is to separate the highly correlated from the less well correlated parameters and to account for the correlations in terms of a small number, preferably two or three hypothetical variables or factors. The principal components analysis was based on a factor model which generates a new set of hypothetical variables that have the property of being uncorrelated. All principal components are needed to reproduce accurately the correlation coefficients of the original variables (Williams, 1978). The correlation matrix was generated from a rectangular data set consisting of values for the parameters of syllable duration, fundamental frequency, pre-

dominant (most intense) harmonic, percent frequency modulation of the harmonics, FM rate, and sweep direction, which was arbitrarily encoded (e.g., 0 for constant frequency, 1 for downsweep, 2 for oscillation, and 3 for upsweep).

We used multidimensional scaling (MDS) as an independent procedure for studying the relationships between different syllable types. The MDS procedure evaluated the correlation of syllable types on the basis of sample means of nine variables (these variables were predominant bandwidth, i.e., peak frequencies in the power spectrum showing at least a 12-dB higher level than the background, FM-FM delay, and peak frequency in a FM, in addition to the ones listed for principal components analysis). The advantage of MDS is that it is a nonparametric procedure and does not make any assumptions regarding normality of the frequency distributions of each variable (Dunteman, 1984). This procedure produces configurations of points obtained by transforming sets of similarity and dissimilarity measures into distances. The coordinates of the configuration are arbitrary in the sense of being only defined up to a central dilation (a uniform expansion or contraction along the coordinate axes), and a rotation, as these transformations in no way effect the monotonicity measure of "goodness of fit." "Goodness of fit" is assessed in terms of the degree of monotonicity between the observed similarity measures and the interpoint distances of the reproduced configuration.

The probability of syllable pairing within call segments was based on a matrix generated by examining the type and frequency of occurrence of consecutive syllable pairs. Over 3000 syllable pairs were examined using RTS. Each syllable was assigned to one of the previously defined syllable types on the basis of its spectral structure. The probability of pairing different syllable types was normalized to the total (paired and unpaired) emissions of that type. The results were represented as a set of histograms.

D. Terminology and taxonomical considerations

We do not yet have a behavioral basis for defining non-echolocation sounds as calls. However, in retrospect, we use "calls" as the general term for describing communication sounds for the following three reasons:

(1) Bats emit these sounds frequently in the presence of one or more conspecifics and rarely when isolated. The calls produced by one bat are directed specifically toward another; some call types are frequently associated with stereotypic body movements, especially wing flicking.

(2) The syllables in these calls are similar to those found in many calls produced by other chiropteran species (Bradbury, 1977; Porter, 1977). Bats' calls are high in frequency and short in duration compared to the calls of nonbat species, but the patterns of their sound spectrograms are strikingly similar to the calls of many other species, including primates (Newman and Wollberg, 1973a; Boinski, 1991).

(3) All of the complex sounds can be decomposed into one or more of 33 types of discrete acoustic units. These may be used in combination or independently in different calls. This type of structural organization is a common feature of communication sounds of birds (Kroodsma, 1977) and other species, as well as of human speech.

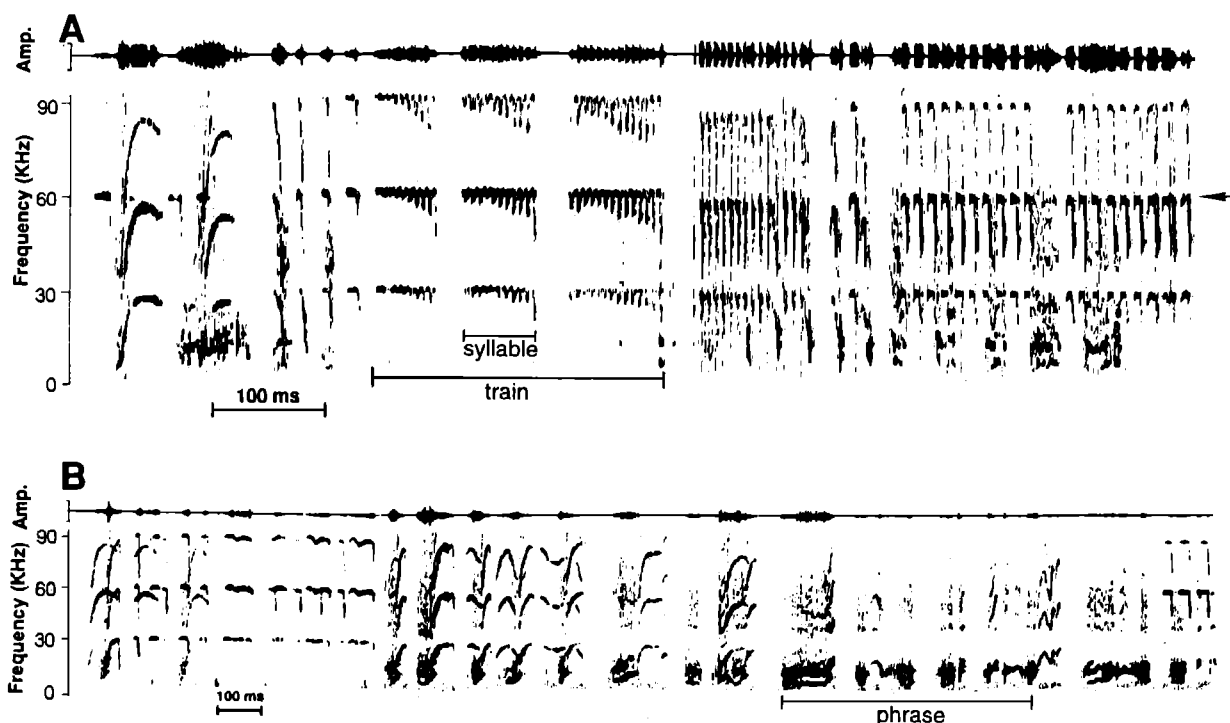


FIG. 2. (a) Sound envelop patterns and spectrograms of calls recorded from a colony of bats in the flight room. Spectra of a simple syllable and a syllable train are labeled. A stream of echolocation pulses (indicated by an arrow) frequently clutters the recording of calls. (b) Sound envelop patterns and spectrograms of an over 1 s long, uncluttered sequence, consisting mostly of simple syllables, of a dialogue between two males as evidenced by head orientation and mouth openings recorded on video. These calls were emitted when three bats (two males and a female) were placed in a small cage. The segment labeled as a phrase is most likely emitted by a single bat because of no overlap and a more or less constant silent interval between different types of syllables.

Calls are distinct from echolocation pulses in their spectra, amplitude envelopes, duration and in the temporal pattern of emission [arrow in Fig. 2(a) shows spectra of echolocation pulses overlapping with calls emitted by other bats in the colony; for an example of the amplitude envelope of an echolocation pulse see Fig. 3(a)]. The echolocation pulses are highly stereotyped because these properties are constrained by the principles of sonar. On the other hand, calls are spectrally diverse and each syllable type exhibits inherent variation in its amplitude modulation and spectral content from one emission to another, i.e., calls are not suitable for the functions of echolocation.

We use the following terminology for describing the structural elements in the calls of the mustached bat. *Syllable*: A discrete part of a call which is surrounded by periods of silence [e.g., see Fig. 2(a)]. By this definition, a syllable in a bat call is equivalent to a syllable in a bird song (Kroodsmma, 1977). Syllables emitted singly constitute a monosyllabic call. In mustached bats, with a few exceptions, a syllable is from 3 to up to 100 ms long. Syllables are further classified as being either "simple syllables," "subsyllables," or "composites." A *simple syllable* consists of a single predominant sound element such as a CF, an FM, or a noise burst (NB). A *subsyllable* is a short segment which is not emitted independently but occurs always in combination with other components in a composite. A subsyllable can be potentially reclassified as a simple syllable, if there is evidence that it is emitted independently. A *composite* consists of a sequence of two or more types of distinct components, each representing a simple CF, NB, or FM pattern, combined

together without any intervening silent interval. As discussed later, each component in a composite corresponds to either a simple syllable or a subsyllable.

All sounds showing a significant modulation ($>20\%$ peak to peak) of any harmonic are "FM" sounds, whereas those having $<20\%$ peak-to-peak modulation are labeled as "CF" sounds. This boundary was established on the basis of a bimodal distribution obtained after pooling data on percent frequency modulation for all simple syllables. A noise-burst ("NB") is defined as a sound which shows no clear fundamental frequency and no clear harmonic structure in its spectral composition (the term noise-burst does not imply Gaussian noise in the sound signal). Simple syllables are named according to the predominant sound type (i.e., CF, FM, or NB) in each syllable. The CF, FM, or NB abbreviation is preceded by a one word description of the geometric pattern of the sound. This prefix is used to define a second characteristic feature of the spectrogram, e.g., "RFM" for "rippled FM" and "DFM" for "downward FM." A lower case prefix is used to further define the three letter abbreviation for a sound spectrogram in the frequency domain, e.g., "dRFM" for "descending RFM."

Another characteristic feature that can be used to distinguish different syllable types is syllable duration. If the duration of the syllable is <50 ms, it is labeled as short, otherwise it is categorized as long. This boundary was also determined by examining the pooled frequency distribution of the duration parameter in all simple syllables regardless of type. A suffix, "s" for short and "l" for long may be included in the abbreviation to define the syllable in the time

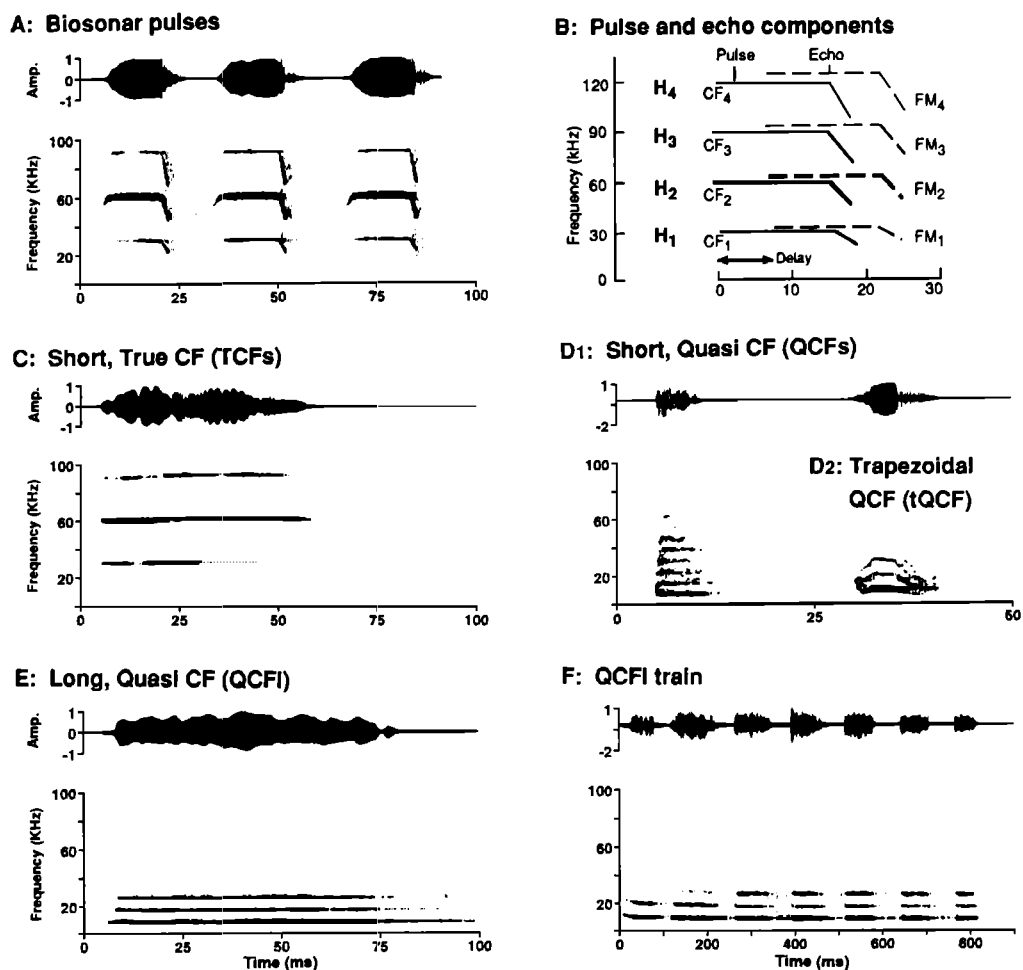


FIG. 3. (a) Sound envelop patterns and spectrograms of echolocation pulses. (b) Schematic of the spectral components in a pulse and echo pair. (c)–(f) Sound spectrograms and sound envelop patterns of the four CF type of simple syllables emitted by the mustached bat. Note the clear difference in spectral and temporal patterns between pulses and calls (TCFs is similar to the CF portion of an echolocation pulse).

domain. However, a three letter combination with either a prefix or a suffix attached was sufficient for distinguishing between the mustached bat's simple syllables. Composites are named as sequential hyphenated combinations of the abbreviations of simple syllables and subsyllables.

A sequence of simple syllables and/or composites were further grouped into high level constructs. These are defined as follows.

Syllable train: A train of syllables of the same type (iso-syllables) in which the silent period between syllables is not longer than the syllable duration [see Fig. 2(a)].

Phrase: A segment taken from a sequence of two or more syllables emitted by a single bat, in which the silent period between any two syllables is roughly similar and may be longer than the duration of any one syllable, but is always less than the total duration of the two syllables surrounding a silent interval [Fig. 2(b)]. Phrases usually consist of different types of syllables and may be equated to the phrase or "segment" in a bird song (Kroodsma, 1977; Marler and Peters, 1988).

Monologue: A series of phrases and/or syllable trains emitted by a single bat and punctuated by one or more silent intervals of variable duration. The duration of the silent in-

terval between phrases is longer than the silent intervals within a phrase or a syllable train.

Dialogue: A combination of phrases that are emitted by two or more bats in a vocal exchange [see Fig. 2(b)].

II. RESULTS

Calls of the mustached bat consist of complex sequences of a rich variety of acoustic elements that are dramatically different from the stereotypic echolocation pulses. This difference is especially evident in calls recorded from a colony of bats in a flight room [Fig. 2(a)]. Even when two or three bats are placed in a cage in a soundproof room, monologues and dialogues are frequently recorded [Fig. 2(b)]. The call sequence shown in Fig. 2(b) was associated with a confrontation resulting from the attempt of one male to place himself between another male and a female. The audio recordings were synchronized with video data on mouth opening and closure to confirm the participation of both bats in a communication episode and further helped to correlate a particular communication sound with the behavior of a bat emitting that sound. Examples of the complex, heterogeneous composition of calls presented here, however, suggest that at this

TABLE II. Mean values of acoustic parameters for “noise burst (NB) type” of syllables.

Parameter	NNBs	NNBI	rBNB
Overall syllable duration (ms)	6.80	325.26	88.00
Base frequency in kHz	6.72	6.80	5.07
Center frequency of predominant band (kHz)	12.50	16.01	8.30
Peak frequency in overall band (kHz)	12.50	25.23	66.72
% scatter of center frequency	82.71	116.61	347.25
Max. bandwidth (kHz)	10.36	18.43	26.96

early stage of studies on this species’ acoustic communication, structural analysis is more important than detailed studies of the behavioral correlates of calls. The results of the structural analysis are the focus of this report.

Our *a priori* classification of acoustic units in calls into several different categories was based upon the patterns of the sound spectrogram. For a more quantitative estimate, however, we used multivariate statistical techniques to estimate the multidimensional boundaries of each type of simple syllable and to reclassify them, if necessary. This allowed us to not only classify syllables into distinct types, but also to assign new syllables to either previously defined or new groups. We quantitatively defined each type of syllable by measuring several parameters (e.g. duration, predominant harmonic frequencies or frequency bands, number of harmonics, the rate and depth of frequency and amplitude modulations, etc.) of syllables obtained from the spectral analysis of a sample of over 300 syllables. This sample was chosen from a qualitative examination of over 2000 syllables on the basis of the “clarity” of their spectra with regard to persisting echoes and overlap of sounds emitted simultaneously by two or more bats. These data, obtained either from bats in a colony or from isolated groups of bats placed in an echo-attenuated cage, were used to calculate the means, standard deviations and the range of variation of each parameter of a syllable and to further characterize and categorize each type of syllable. According to our scheme, simple syllables are grouped according to the types of predominant sound components, i.e., CF, FM, or noise bursts, and further classified according to additional features of the sound spectrogram. Quantitative data for parameters characterizing each type of simple syllable are presented in Tables I, II, and III. A list of abbreviations along with reference to illustrations, wherever applicable, is provided in the Appendix. In the first section, all of the simple syllables are described. This is fol-

TABLE III. Mean values of acoustic parameters for upward and downward FM syllable types.

Parameter	bUFM	bDFM	cDFM
Overall syllable duration (ms)	27.45	7.55	3.71
Frequency of fundamental (<i>f</i> ₀) in kHz	23.04	12.17	24.00
Peak of fundamental frequency (kHz)	28.14	16.34	31.33
Frequency of predominant harmonic (kHz)	46.07	12.17	48.00
% frequency modulation in harmonics	59.86	50.17	46.98.33
Max. FM depth for <i>f</i> ₀ (kHz)	10.20	8.34	14.66
FM sweep rate in <i>f</i> ₀ (max. kHz/ms)	0.96	1.14	4.29
Delay between consecutive FM sweeps (ms)	—	32.68	9.33

lowed by a detailed statistical analyses of the inherent variation within and among the different types of simple syllables in order to determine the boundaries of their spectral parameters. The inter-relationship between syllable types is visualized using the statistical technique of MDS. Finally, composites are described and shown to consist of two or more distinct components. Most of these components are similar to the simple syllables that are emitted independently. Transition analysis of syllable pairs within phrases reveals that phrases are constructed from rule-based combinations of syllables.

A. Classification and description of simple syllables

1. Constant frequency (CF) syllables

CF syllables can be grouped into two categories; those that are true CF (TCF) and those that are quasi-CF (QCF). In TCF syllables, the frequency does not vary more than 10% over at least 80% of the syllable duration. In QCF syllables, the frequency modulation ranges between 10% and 20%. In the mustached bat, TCF syllables consists of one type, namely, short TCF (TCFs) and QCF consists of three types, namely, short QCF (QCFs), long QCF (QCFL), and trapezoidal QCF (tQCF). QCFs and QCFL are distinguished primarily on the basis of syllable duration and tQCF is characterized by the shape of its sound spectrogram. The parameters of each syllable are presented in Table I and examples of sound spectrograms are shown in Fig. 3. A brief description of each type follows (see Table I for a quantitative comparison).

a. *TCFs*. This syllable is very similar to the CF component of the echolocation signal [Fig. 3(c)]. It is short (38.4 ± 8.7 ms; $n=29$) with respect to communication sounds, but is longer than the echolocation CF. The example shown is a relatively long TCF. This echolocation pulse-like CF syllable has a mean fundamental frequency of 30.4 kHz with 3 harmonics and a peak to peak frequency modulation of <2%. It consists of at least three harmonics; the second harmonic near 60 kHz is the most intense as in the echolocation pulse CF. The fundamental of TCFs is 12 dB weaker than the second harmonic; whereas in the echolocation pulse CF, it is 34–36 dB weaker than the second harmonic.

b. *QCFs*. This syllable is very short (11.0 ± 3.2 ms; $n=10$). The fundamental at 8.6 ± 1.6 kHz ($n=10$) is the most intense, whereas the second harmonic is typically 10 dB lower [Fig. 3(d)1]. Higher-order harmonics show a trend of decreasing intensities (approximately 4 dB per octave for each successive harmonic). It consists of 6–8 harmonics although the highest frequency of QCFs is ~65 kHz, but the predominant (highest intensity) components (in this case, about 20 dB more intense than the fundamental) hardly go beyond 30 kHz.

c. *QCFL*. This syllable is very long (302.4 ± 197.4 ms; $n=30$) in contrast to the QCFs and shows a significantly greater amount of modulation (about 3.5%) than TCFs. The mean of the fundamental frequency is about 8 kHz and the number of harmonics range from 3 to 7 so that its bandwidth rarely extends beyond 60 kHz [Fig. 3(e)]. Typically, only the first three harmonics are strong. A QCFL train may consist of a series of up to 7 or 8 QCFL syllables and is nearly 1 s long

with an intersyllable silent interval of a few ms [Fig. 3(f)]. To the human ear, this sounds as a short melodious whistle.

d. iQCF. This syllable is characterized by a ramped increment in frequency during its initiation and a similar ramped decline in frequency prior to termination [Fig. 3(d)2]. The middle plateau portion constitutes over 80% of the duration of the syllable. Other than the ramped “step-up step-down” pattern, this syllable is very similar to QCFs in its duration (14.1 ± 4.1 ms; $n=9$), fundamental (8.9 ± 1.0 kHz; $n=9$), and energy distribution over different harmonics. The overall bandwidth, i.e., number of harmonics is usually restricted to about half the number observed in QCFs.

2. Noise burst (NB) syllables

NB syllables consist of narrow-band (NNB) and broad-band (BNB) noise bursts. NNB shows a predominant bandwidth of $<20\%$ of the value of the center frequency, whereas BNB shows a predominant bandwidth of $>20\%$ of the value of its center frequency. NNB's may be either short (NNBs) or long (NNBI). Three types of NB's are frequently emitted namely, short NNB (NNBs), long NNB (NNBI) and rectangular BNB (rBNB). A quantitative comparison of the important parameters is shown in Table II.

a. NNBs. This syllable is very short (6.8 ± 2.8 ms; $n=10$) [Fig. 4(a)]. It has an initial bandwidth of about 10 kHz which gradually decreases to less than 1 kHz.

b. NNBI. This syllable is long (325.3 ± 176.5 ms; $n=23$) and has peak energy below 20 kHz [Fig. 4(b)]. The overall bandwidth of this signal varies from 13 to 25 kHz.

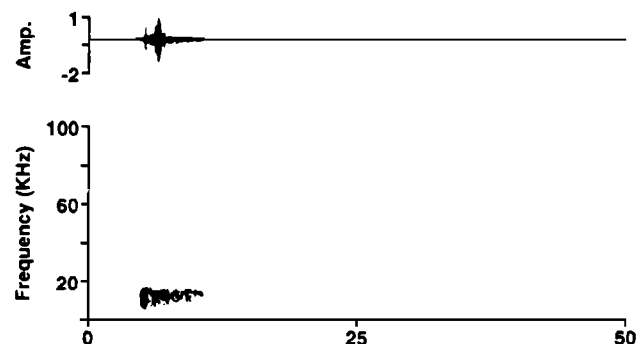
c. rBNB. This is a broadband, short duration (mean length of 88 ms) noise burst which sometimes has a few cycles of intermittent sinusoidal frequency modulation embedded within the noise [Fig. 4(c)]. BNB is further characterized by a filled rectangular shape of the sound spectrogram. This distinguishes it from the trapezoidal and other shapes of BNB's observed in other species.

3. Frequency-modulated (FM) syllables

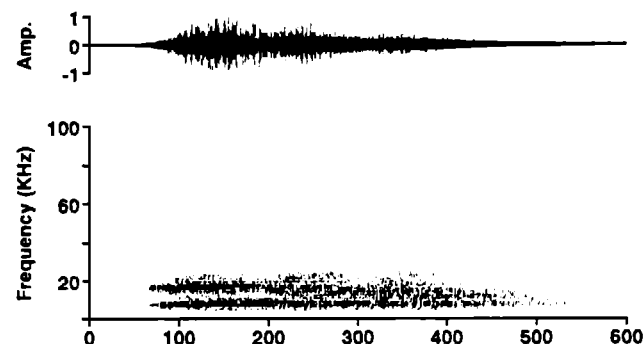
FM sounds comprise the largest variety of syllable types. In FM syllables, frequency varies by $>20\%$ of the mean frequency of a single harmonic. Frequency modulations can be predominantly unidirectional (upwards or downwards) or bidirectional. Unidirectional FM is defined as an FM that sweeps in one direction $>80\%$ of the total depth of the FM sweep and any FM in the opposite direction must not last for $>50\%$ of the total duration of the syllable.

On the basis of sweep direction, FM sounds are grouped into seven different categories. The first two categories named as, (1) upward FM (UFM), (2) downward FM (DFM) are unidirectional, whereas the remaining five, namely, (3) arched FM (AFM), (4) humped FM (HFM), (5) rippled FM (RFM), (6) sinusoidal FM (SFM), and (7) wrinkled FM (WFM), are bidirectional. Except for UFM and HFM, all other categories are further divided into two syllable types. The sole examples of UFM and HFM are the bent UFM (bUFM) and single HFM (sHFM), respectively.

A: Short, Narrowband NB (NNBs)



B: Long, Narrowband NB (NNBI)



C: Rectangular Broadband NB (rBNB)

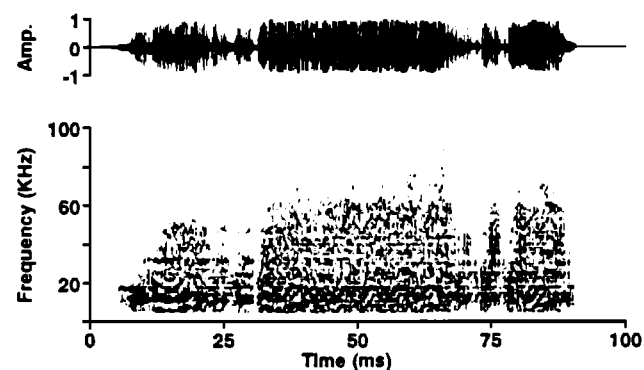


FIG. 4. Sound envelop patterns and spectrograms of the three noise-burst (NB) type of simple syllables emitted by the mustached bat.

4. Upward frequency modulation (UFM)

a. bUFM. This sole type of the UFM category consists of syllables which are 27.4 ± 8.0 ms ($n=11$) long and have 3 to 4 harmonics [Table III, Fig. 5(a)]. The fundamental frequency in bUFM sweeps upward asymptotically from below 20 to nearly 30 kHz. Frequently, the second harmonic in a bUFM may terminate in a small but sustained downward sweep lasting from about 5 to 20 ms, so that the duration of the consistent portion of bUFM is about 15 ms. The short terminal FM sweeps down from near 30 to roughly 25 kHz. This downward sweeping component (a small terminal dip) is usually attenuated by at least 50 dB in the fundamental and third harmonic.

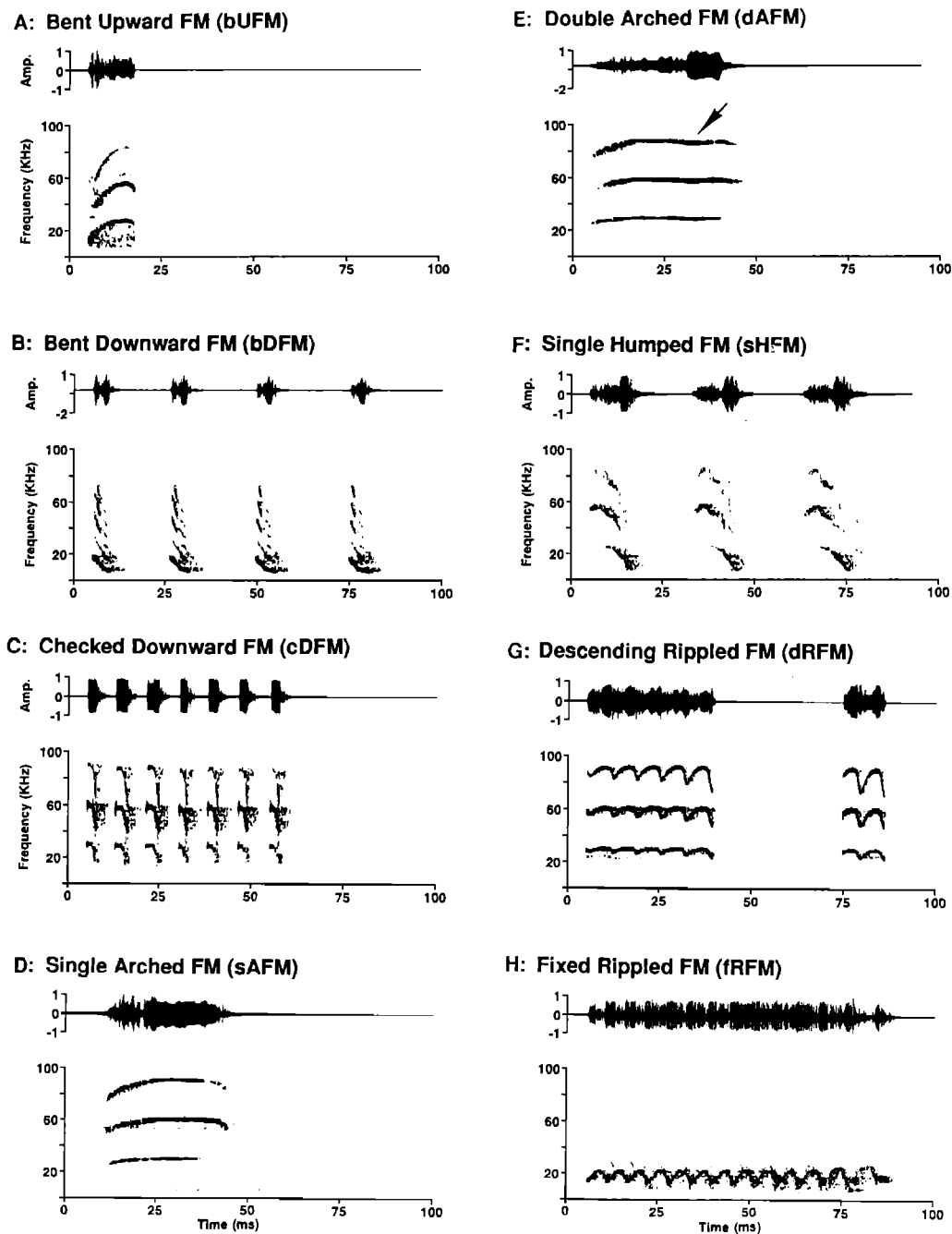


FIG. 5. Sound envelop patterns and spectrograms of the eight FM type of simple syllables emitted by the mustached bat. cDFM and dRFM are labeled as “echolocation pulse-like” syllables, whereas sAFM, dAFM, and TCFs (see Fig. 3) are labeled as “pulse CF-like” syllables.

5. Downward frequency modulation (DFM)

Two types of DFM syllables namely, (i) bent DFM (bDFM), and (ii) checked DFM (cDFM) were recorded. A quantitative comparison of these is provided in Table III.

a. bDFM. This syllable is very short (7.5 ± 1.7 ms; $n=31$) and is always emitted as a train of 4 to 5 syllables [Fig. 5(b)]. The fundamental frequency sweeps down from about 20 to 10 kHz and has 4 to 6 harmonics. The sound spectrogram is characterized by a reduction in the bandwidth in the relatively flat second half of the downward sweep.

b. cDFM. This is the shortest FM syllable (3.7 ± 1.1 ms;

$n=27$). It always occurs in a train of 5 to 10 syllables [Fig. 5(c)]. Each syllable has a 1- to 2-ms-long upward FM segment prior to a deep, linear downward FM sweep so that its sound spectrogram appears as an inverted check mark. The presence of harmonics at 30, 60, and 90 kHz makes it similar to the “terminal buzz” of a sequence of echolocation pulses emitted during the terminal phase of insect pursuit. As in the echolocation pulse, the second harmonic predominates, but the fundamental and second harmonic are only 10 and 3 dB weaker, respectively than the second harmonic. This syllable is emitted in nonflying situations.

TABLE IV. Mean values of acoustic parameters for arched, humped, and rippled FM syllable types.

Parameter	sAFM	dAFM	sHFM	fRFM	dRFM
Overall syllable duration (ms)	27.33	49.67	13.43	72.15	57.93
Frequency of fundamental (f_0) in kHz	28.07	29.48	15.95	13.68	28.64
Peak of fundamental frequency (kHz)	29.50	30.57	23.14	19.64	30.55
Frequency of predominant harmonic (kHz)	56.13	58.97	46.28	13.68	57.27
% frequency modulation in harmonics	12.76	8.50	89.90	54.84	30.56
Max. FM depth for f_0 (kHz)	3.22	2.17	14.38	11.16	8.75
FM sweep rate in f_0 (max. kHz/ms)	0.40	0.64	2.56	3.33	4.95
Delay between consecutive FM sweeps (ms)	–	–	32.22	5.96	7.15

6. Arched frequency modulation (AFM)

AFM consists of (i) single AFM (sAFM), and (ii) double AFM (dAFM). As the name implies, the number of arches is the only feature that distinguishes these two types of AFM syllables.

a. sAFM. This is a short duration (27.3 ± 8.4 ms; $n = 6$) FM syllable in which the fundamental frequency gradually increases from approximately 28 to 31 kHz and then similarly decreases [Fig. 5(d)]. The duration of the upsweep in a syllable was generally similar to that of the downsweep. Four harmonics are usually observed with the second harmonic in the 60-kHz region being predominant.

b. dAFM. This syllable is also a short (49.7 ± 13.4 ms; $n = 6$) frequency-modulated syllable whose spectrogram shows a sequence of two shallow arches with a small dip near the middle or at about two-thirds of the duration of the syllable [Fig. 5(e) arrow]. dAFM can be nearly twice as long as sAFM. The peak and fundamental frequencies are very similar to those of sAFM. Four harmonics are usually observed, with a predominant second harmonic. Although bUFM, sAFM, and dAFM may appear to be spectrally similar, they are statistically different in that the fundamental of the bUFM typically starts at about 10 kHz lower than that of the sAFM and dAFM. Also, TCFs may be attached to bUFM but not to sAFM or dAFM.

7. Humped frequency modulation (HFM)

a. sHFM. This syllable is short (13.4 ± 2.4 ms ($n = 30$)). In sHFM, a small initial upsweep is followed by a large downsweep with a “hump” at about 25 kHz [Table IV, Fig. 5(f)]. The downsweep terminates near 10 kHz (mean of 8.8 kHz ± 1.0 , s.d.). Occasionally a short plateau portion is present in the middle of the downsweep. This syllable is frequently emitted as a train of 3 to 4 isosyllables. The total number of harmonics also varies from 3 to 4.

8. Rippled frequency modulation (RFM)

RFM consists of descending RFM syllables (dRFM) and fixed RFM syllables (fRFM). Quantitative data for different parameters of these syllables are presented in Table IV.

a. dRFM. The spectrogram of this syllable shows a sequence of ripples with a gradation in the depth of the downward frequency modulation so that the depth of the downward sweep increases with each cycle [Fig. 5(g)]. The final downsweep in the second (predominant) harmonic has a depth of about 15 kHz and sweeps downward at a rate of

nearly 5 kHz/ms. This syllable typically shows three harmonics and the peak of the fundamental frequency is near 30 kHz. dRFM frequently occurs as a train of variable length (57.9 ± 22.8 ms; $n = 30$) syllables. The number of ripples dictates the total duration of each syllable.

b. fRFM. fRFM also shows a sequence of oscillations or ripples, where the ripples resemble a rectified sinusoidal or a quasicycloid function [Fig. 5(h)]. The amplitude of the fundamental is higher than other harmonics by about 50 dB. The mean frequency level in the ripples of the fundamental is fixed at about 15 kHz. The peak and trough frequencies of the ripples are about 10 to 25 kHz and the valley time is relatively short. The ripples may show an increase in magnitude toward the end of the syllable. The mean duration of the entire syllable is 72.1 ± 13.4 ms ($n = 13$). The mean of the overall bandwidth of the call is 45 kHz but the predominant bandwidth is limited to 10 kHz. The rate of the frequency oscillation at about 160 Hz is significantly higher than that of dRFM, although the FM sweep rate at approximately 3 kHz/ms in the fundamental is significantly lower than that of dRFM.

9. Sinusoidal frequency modulation (SFM)

SFM consists of fixed SFM syllables (fSFM) and quasi-SFM syllables (qSFM). fSFM shows different gradations of “noisiness” in the SFM pattern, whereas qSFM contains short QCFs segments inserted at different loci within the SFM pattern. Other features of these syllable types are quantitatively compared in Table V and briefly described below.

a. fSFM. This is relatively long (89.5 ± 11.7 ms; $n = 17$) and shows sinusoidal frequency modulation at a rate of 195.2 ± 15.6 Hz [Fig. 6(a)]. “Fixed” implies a relatively small overall variation in the depth and rate of oscillations. The fundamental frequency is relatively low (12.8 ± 1.3 kHz). The number of harmonics is highly variable. The mean overall bandwidth is 66 kHz, whereas the predominant bandwidth is limited to 30 kHz. Bandwidth and duration characteristics were therefore similar to rBNB, which may be considered an extreme variant of a noisy fSFM. Unlike rBNB, in fSFM amplitude modulation was pronounced.

b. qSFM. This syllable consists of sinusoidal frequency modulations similar to fSFM (duration = 76.4 ± 9.0 ms and fundamental frequency = 11.6 ± 0.3 kHz; $n = 5$). However, the rate of frequency modulation within a single syllable may vary and the sinusoidally frequency modulated pattern may be ramped upward or downward or interrupted by short QCF segments [Fig. 6(b)]. The average rate of oscillation (192.7

TABLE V. Mean values of parameters for sinusoidal and wrinkled FM syllable types and echolocation pulses.

Parameter	fSFM	qSFM	WFMI	WFM	Pulse
Overall syllable duration (ms)	89.53	76.40	154.60	19.10	20.00
Frequency of fundamental (f_0) in kHz	9.21	11.62	7.97	7.01	26.60
Peak of fundamental frequency (kHz)	11.22	15.19	9.67	8.58	29.47
Frequency of predominant harmonic (kHz)	42.82	61.47	42.36	41.40	21.58
% frequency modulation harmonics	18.41	11.62	8.63	14.01	53.20
Max. FM depth for f_0 (kHz)	4.03	7.15	2.88	3.01	5.74
FM sweep rate in f_0 (max. kHz/ms)	1.57	1.48	0.05	1.28	1.99
Delay between consecutive FM sweeps (ms)	5.12	5.23	—	4.90	12.00

± 6.8 Hz) is not significantly different from fSFM. No consistent feature of this SFM pattern can be elucidated from the limited number of syllables available for analysis. qSFM, therefore, is structurally one of the most polymorphic syllables.

10. Wrinkled frequency modulation (WFM)

“Wrinkling” refers to an irregular frequency modulation as seen in the sound spectrogram. WFM syllables consist of two types: (i) short WFM (WFM), and (ii) long WFM (WFMI). These are briefly described below and the mean values of various parameters measured for these syllable types are listed in Table V.

a. WFM. This is short in duration (19.1 ± 6.0 ms; $n = 29$) and is emitted as a train of 4 to 22 syllables [Fig. 6(c)]. WFM has several harmonics and shows a mean overall bandwidth of 59 kHz and a predominant bandwidth of 24 kHz. It shows an irregular pattern of frequency modulations. However, syllable duration, fundamental frequency and the percent frequency modulation of the harmonics are very similar.

b. WFMI. Unlike other simple syllables, WFMI is a heterogeneous group of medium to long duration syllables showing a relatively shallow wrinkling over a mean duration of 154.6 ± 52.9 ms ($n = 11$). Parameters defining WFMI exhibit large variation from the mean. The example shown in Fig. 6(d) is somewhat atypical in the overall pattern of modulation and is shown because it was the only one available whose spectrogram was not cluttered with echolocation signals. Most syllables showed either an overall rise or a fall in the mean frequency of the harmonics. It is important to note that all members of this type (except the one illustrated) were recorded from bats in a large colony in the flight room.

B. Internal relationships of syllable parameters: Principal components analysis

Discriminant analysis provides statistical validation for a classification and allocation scheme for each example of a syllable type, but cannot show the overall inter-relationship of multiple parameters obtained by pooling samples of all syllable types. The distribution of the mean values of two parameters (fundamental and predominant frequencies) is shown in Fig. 7(a) and (b), respectively. With the exception of TCFs, the fundamental frequencies of all CF syllables and predominant frequencies of NB syllables are much lower (< 20 kHz) than that of echolocation pulses. FM syllables show somewhat higher fundamentals (between 10 and 30

kHz), although the lowest frequencies in these FM syllables are lower than 24 kHz, which corresponds to the terminal frequency of the downsweep in an echolocation pulse. TCFs, sAFM, dAFM, and dRFM have similar mean fundamental and predominant frequencies as echolocation pulses, whereas cDFM shows a similar pattern with a slightly lower fundamental. cDFM and dRFM are labeled as “echolocation pulse-like” syllables, and TCFs, sAFM, and dAFM are labeled as “pulse-CF-like” syllables.

To view the grouping of simple syllabic variants as a function of all of the measured parameters, we employed principal components analysis of a multivariate model, in which six parameters were included (these parameters were syllable duration, fundamental frequency, normalized percent FM of harmonics, FM rate, predominant frequency, and sweep direction). Two-dimensional plots of the first and the second or third principal components showed the relative scatter of all variants. We superimposed the discriminant classification scheme onto the scatter plots so that each quantified example of a syllable is allocated to a syllable group or type denoted by a different symbol or letter of the alphabet. Assuming a Gaussian distribution, bivariate confidence intervals are drawn at the 75% confidence level on the centroids of the scatter plot. The ellipse produced for each syllable type is centered on the sample means of the two factors and is shown for the first and second and first and third principal components in Fig. 8(a) and (b), respectively. Its major axis is determined by the unbiased sample standard deviations on each axis, and its orientation is determined by the sample Pearson correlation between factors plotted on the X and Y axes. The orientation, overlap and size of the ellipses reflects the intergroup separation and the inherent variation within each syllable-type as represented in the multidimensional space. It should be pointed out that a small scatter for some of the syllables (e.g., TCFs) may result from a relatively small sample. Placement of syllable types along the first principal component does not follow the ordering of any single parameter and is probably associated with a combination of several frequency parameters. The placement of syllable types along the second and third principal components suggests that these components are primarily associated with syllable duration and sweep direction, respectively.

This procedure accommodated nearly 80% of the variation in three dimensions and about 68% of the variation in two dimensions. A “scree” plot revealed that three-dimensional (-component) solutions are satisfactory. Our data show that in general, the CF type of sounds are more

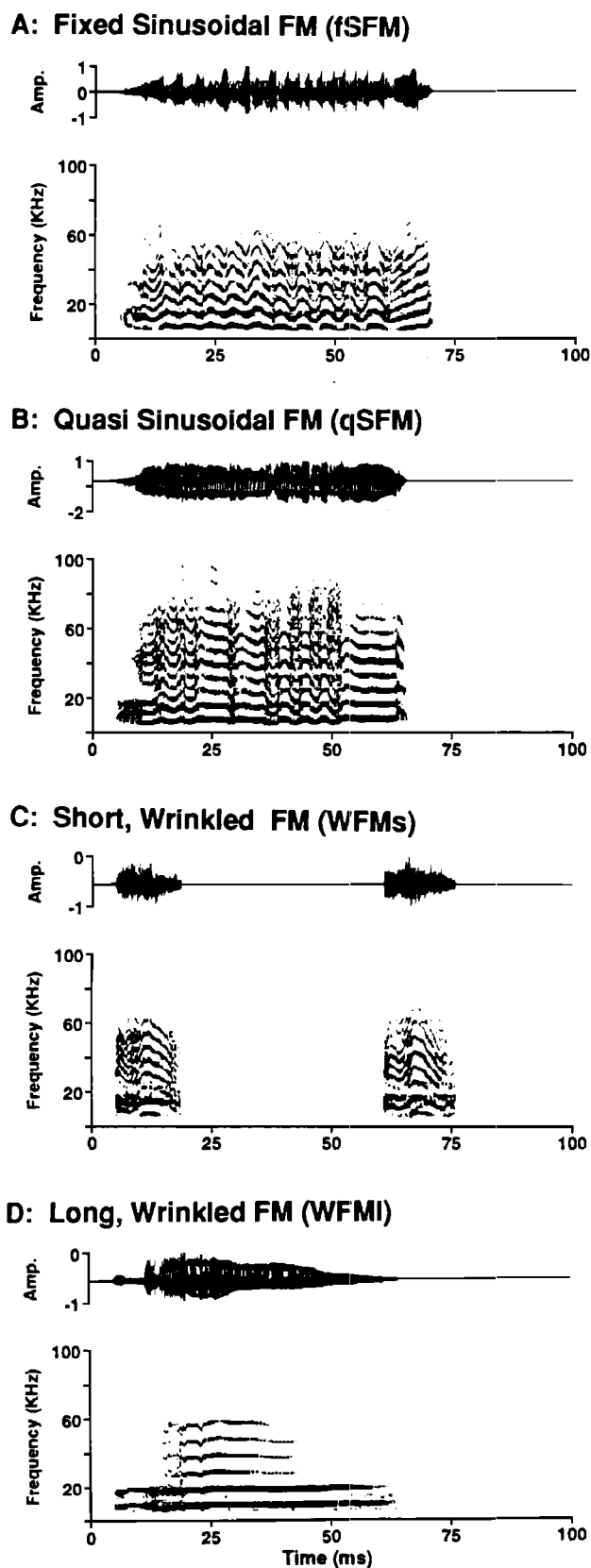


FIG. 6. Sound envelop patterns and spectrograms of the four, sinusoidal and wrinkled, FM type of simple syllables emitted by the mustached bat.

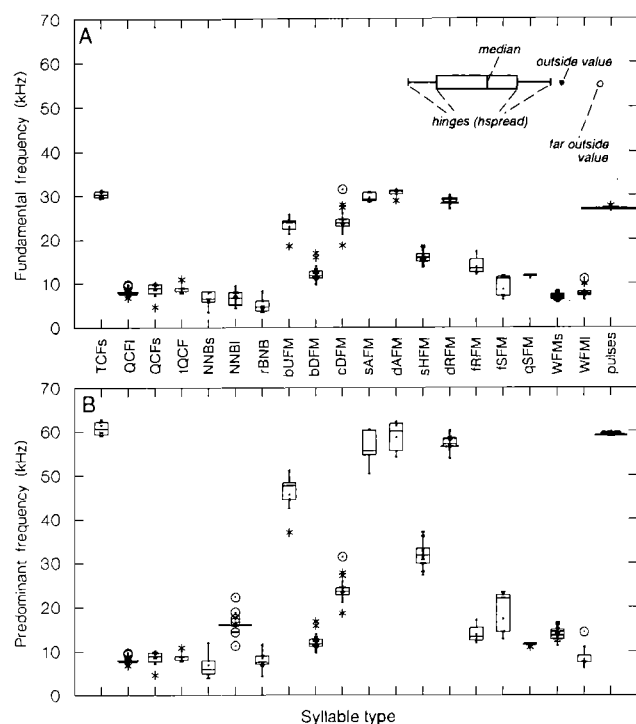


FIG. 7. A series of jittered density plots superimposed upon box plots of the distributions of (a) the fundamental frequency and (b) the predominant frequencies in samples representing each syllable type. Note that the fundamental and the predominant frequency components in the majority of syllables are below 30 kHz. Overlap between each parameter in the different types of simple syllables is apparent. Key: The horizontal line within the box represents the median for the sample. The inner fences or horizontal edges of the box represent 1.5 times the H -spread which is equivalent to the interquartile range or mid range around a mean and the outer fences of the whiskers represent three times the H -spread. Asterisks represent outside values and circles denote far outside values, relative to the H -spread.

tightly clustered than the broadband and FM type of sounds, perhaps because fewer independent variables are involved. For example, FM depth and rate are virtually absent in the CF type of syllables. Thus TCFs, QCFs, and tQCF are the most tightly clustered syllable types, whereas QCFI is somewhat loosely clustered along the second and third principal components, primarily because of the large variability in the duration parameter of this syllable type. The first two principal components account for most of the variation in cDFM, whereas bUFM and fRFM are loosely organized along all three component axes. NNBI shows the largest overall dispersion among the noise-burst type of syllables. Among the FM type of syllables, WFMs shows very tight grouping along all three component axes. The multivariate analysis also shows that several of the measured parameters covary, e.g., fundamental frequency and sweep direction are more closely correlated to each other than with the overall duration and percent modulation.

Fortuitously, in one recording from two bats the fSFM was frequently emitted by a single bat and provided a means for analyzing one of the possible sources of acoustic variability within a syllable type. The results indicate that much of the variation in fSFM can be accounted for by the variability of sounds produced by the same bat (Table VI). However, a large standard deviation of parameters in the monosyllabic

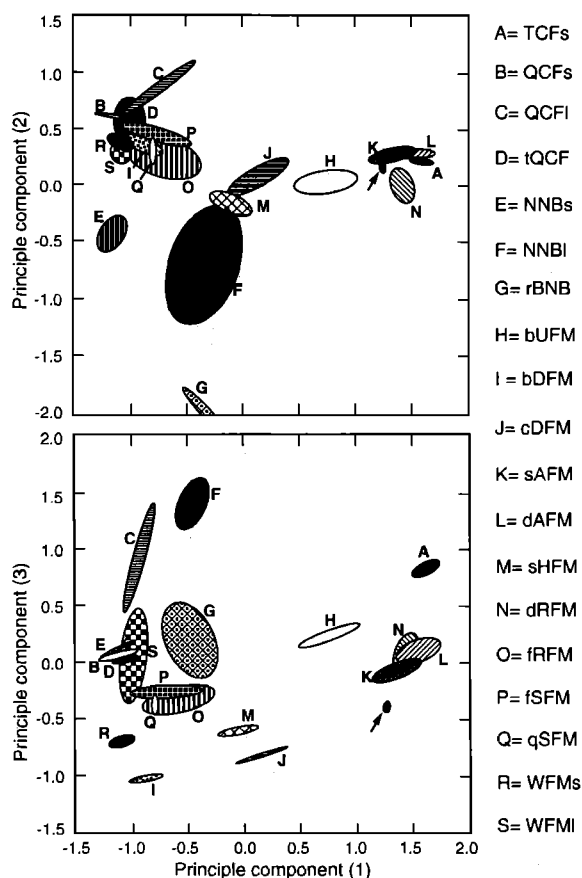


FIG. 8. (a) Top panel: Bivariate sample ellipsoids drawn at the 75% confidence interval based on scatter plots of the first two principal components of a three-dimensional solution for the multivariate parameters of syllables (plotted with small size letters). (b) Bottom panel: Bivariate sample ellipses drawn at the 75% confidence interval for each syllable type (indicated by large size letters) based on scatter plots of simple syllables for the first and third principal components. Echolocation pulses (indicated by an arrow), are the most tightly grouped of all vocalizations. For an explanation of syllable abbreviations see the Appendix.

fSFM calls of a single bat may partly result from the smaller sample ($n=11$) available from a single bat compared to the large sample ($n=31$) available from several bats in the colony. Only one parameter, the variability in the percent frequency modulation of harmonics was larger for numbers

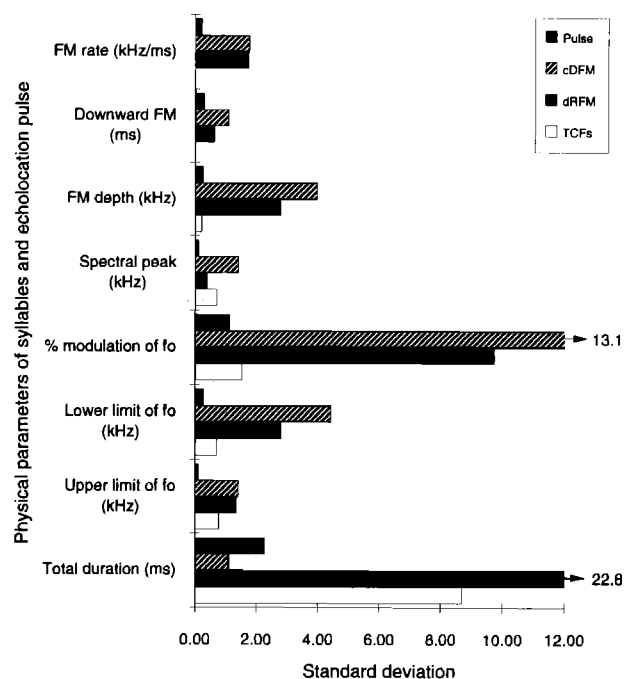


FIG. 9. A histogram of the sample standard deviations of several parameters, labeled on the x axis, of an echolocation pulse compared to two "echolocationlike" syllables (dRFM, cDFM), and TCFs.

pooled from several bats as compared to those obtained from a single bat.

Data on echolocation pulses obtained from previous studies (Fitzpatrick *et al.*, 1991) were included in the scatter plot of the first and second or third principal components for a comparison of the two types of species-specific sounds produced by the mustached bat. An extremely tight plot of a sample of 50 echolocation pulses, indicated by the arrow in Fig. 8(a) and (b), clearly demonstrated the stereotypic nature of the echolocation signals relative to calls. Echolocation pulses appear adjacent to dRFM, which is spectrally similar to an echolocation pulse. TCFs, sAFM and dAFM also contain pulse CF-like components and were also plotted in the three-dimensional neighborhood of echolocation pulses. The difference in variation between echolocation pulses and syllables is further illustrated by the bar chart in Fig. 9, where the standard deviation for eight different parameters for

TABLE VI. Variation in the acoustic parameters in fSFM produced by a single bat and that produced by many bats.

Syllable descriptor	One bat			Many bats		
	Mean	$\pm$ S.E.	Range	Mean	$\pm$ S.E.	Range
1. Overall syllable duration (ms)	89.53	11.75	66.0–109.0	66.85	7.15	55.5–76.5
2. Frequency of fundamental (f_0) in kHz	9.21	2.15	6.4–13.3	12.84	1.34	10.14–15.79
3. Peak of fundamental frequency (kHz)	11.22	2.87	7.4–17.5	16.70	1.45	14.1–19.9
4. Frequency of predominant harmonic (kHz)	18.41	4.30	12.8–26.6	12.84	1.34	10.1–15.8
5. % frequency modulation in harmonics	42.82	9.73	26.0–63.0	59.54	14.82	21.7–91.4
6. SFM rate (cycles/s)	195.18	15.60	180.0–247.0	188.23	8.53	161.0–200.0
7. Overall bandwidth (kHz)	60.24	18.37	30.3–86.0	42.78	6.55	34.0–62.1
8. Max. FM depth for f_0 (kHz)	4.03	1.58	1.9–8.4	7.55	1.89	3.4–12.5
9. FM sweep rate (max. kHz/ms)	1.57	0.63	0.7–3.4	1.42	0.37	0.6–2.4
10. Upward sweep duration (rise time; ms)	2.58	0.18	2.0–2.8	5.32	0.27	5.0–6.2

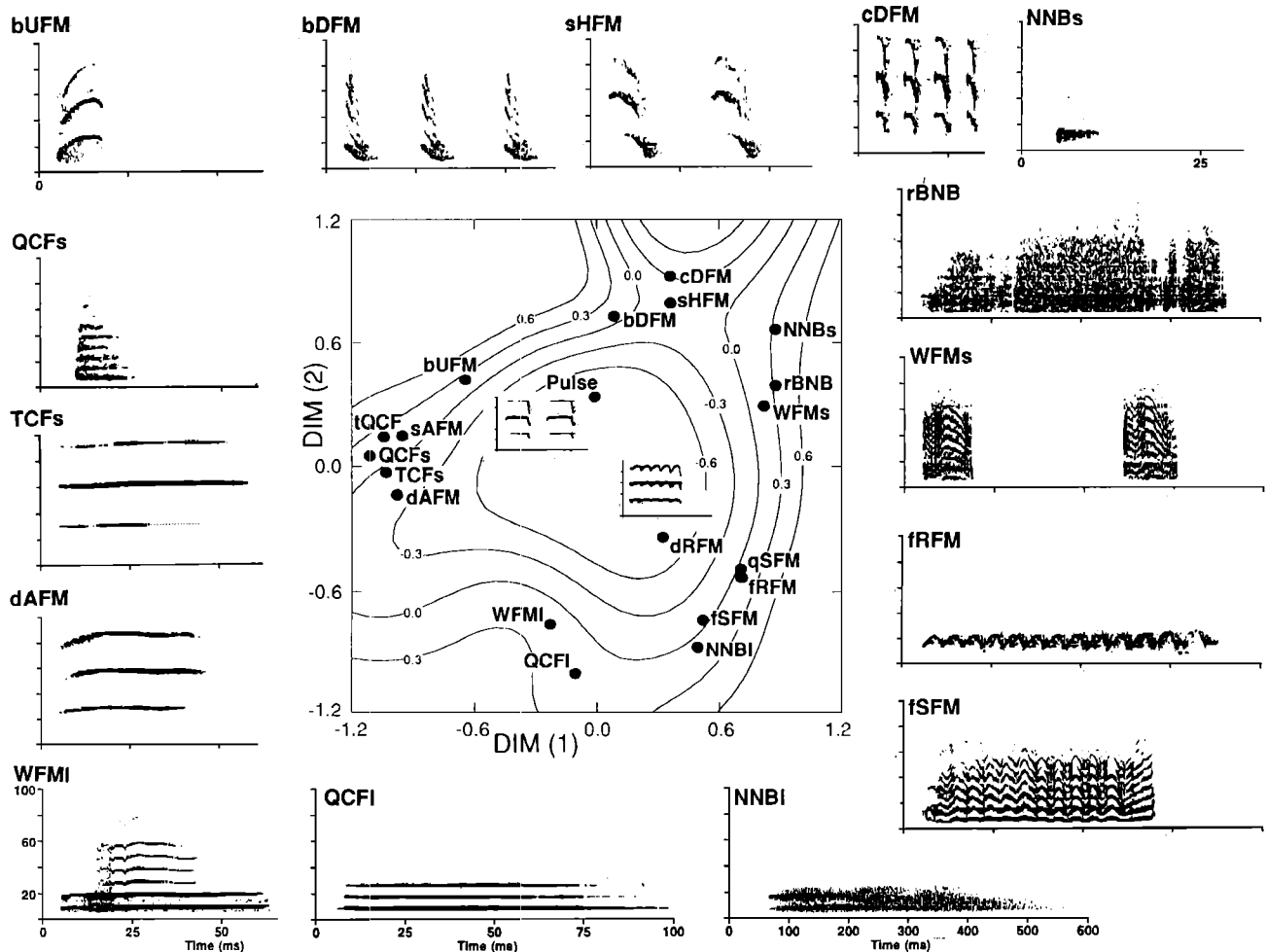


FIG. 10. Multidimensionally scaled (MDS) configuration of syllable types and echolocation pulses obtained from mean values of nine parameters, with no missing values. The third dimension is represented by a contour plot. Spectrograms for most syllable types are also shown around the perimeter of the MDS plot. All unlabeled spectrograms around the perimeter of the MDS plot are drawn to the same scale as WFI. Spectrograms for the echolocation pulse (also included in the model) and dRFM are shown at the center of the contour plot. Note the separation of CF and CF-like syllables from FM syllables.

echolocation pulses are compared with that for dRFM and pulse CF-syllables, namely, TCFs, sAFM, and dAFM.

C. Multidimensional scaling (MDS) of syllables types

Principal components analysis shows the association between syllables as a function of the relationship between the hypothetical parameters generated from multivariate data. In other words, each syllable is plotted on the basis of multiple parameters regardless of its affiliation to a group, and discrete measures of intergroup distances cannot be calculated from this analysis alone. In Fig. 8(a) and (b), a classification scheme based on multivariate discriminant analysis is superimposed on these plots to give a general idea of the relationship between syllable types. For example, from the principal components analysis alone, it is not clear if in a multidimensional space, dRFM is closer to cDFM than to WFMs. In fact, dRFM is close to cDFM with respect to its predominant frequency and the depth of the downward sweeping FM, but is closer to fRFM in other dimensions such as fundamental frequency, syllable duration and FM rate. Similarly, one may question whether WFMs is spectrally closer to sHFM than to bDFM and if so, by how much.

For MDS of simple syllables, we used the mean values for each parameter of all syllable types to calculate the maximal distances between each syllable type and utilized this distance data to generate a three-dimensional plot. Amplitude modulation, although pronounced for some syllables, was not used in the categorization scheme nor quantified for this analysis because their amplitude envelopes exhibited summation effects in the background of echolocation sounds, even though their spectra were distinct enough to be quantified. The fit of configuration distances to original data was extremely close, as evidenced by the low coefficient of alienation (Kruskal, 1964) and a clean Shepard diagram (Wilkinson, 1990). Fitting a monotonic regression function in two dimensions captured 89% of the variation between syllable types, whereas fitting the same function in three dimensions captured over 99% of the intertype variation (Fig. 10). MDS revealed a roughly circular configuration of syllable types in the first two dimensions. Addition of a third dimension represented by a contour plot, revealed a shallow bowl-shaped configuration with the central region representing the bottom of the bowl. This helped to further discriminate between types that were plotted relatively close to each other in the

first two dimensions. The MDS configuration generally separated syllable types with a predominant CF component from those containing noise-bursts or an FM component. NNBI, however, was placed closer to fSFM and fRFM than to rBNB or NNBs. Furthermore, scaling of multivariate data to one dimension gave the following sequence of syllable types: QCf, QCfI, TCf, dAFM, sAFM, tQCF, WFMI, bUFM, bDFM, dRFM, sHFM, cDFM, WFMs, fSFM, qSFM, fRFM, NNBs, rBNB, and NNBI. This ordering of syllable types is useful for experimental studies where all syllable types have to be systematically delivered in a sequence.

D. Composites

Composite syllables or “composites” are made up of two or more distinct components that are combined without an intervening silent interval. Altogether, we have identified 14 different types of composites. Of these, two composites consist of a combination of three distinct components. In the remaining three composites, however, one of the syllables is a subsyllable, i.e., it cannot be categorized as a simple syllable.

The different types of composites are named according to the empirically established combination of simple syllables and abbreviated accordingly. For the purposes of description these are grouped according to the sequence in which the basic types of sounds are combined. Thus, there are three CF-FM, five FM-CF, three FM-FM, one NB-FM, one FM-NB, and one FM-FM-CF type of combination in the composites (Figs. 11 and 12). These are described below.

1. CF-FM combinations

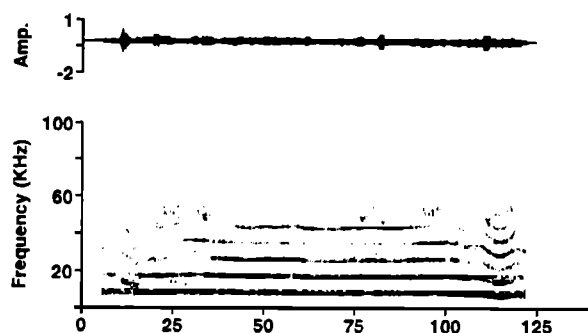
The three composites included in this category contain combinations of a subsyllable and a simple syllable. These composites are named as QCfI-paraboloid UFM syllable (QCfI-pUFM), QCfI-paraboloid DFM syllable (QCfI-pDFM), and QCfI-bent UFM syllable (QCfI-bUFM).

a. QCfI-pDFM. This is a long (105.7 ± 7.5 ms; $n=4$) composite consisting of a flat QCfI-like component followed by a 21% downward modulation of the fundamental frequency in the pDFM subsyllable [Fig. 11(a)]. The initial and terminal frequencies are similar, but toward the end of the composite the frequency transiently dips down by nearly 2 kHz. The total duration of a pDFM subsyllable is only about 12 ms.

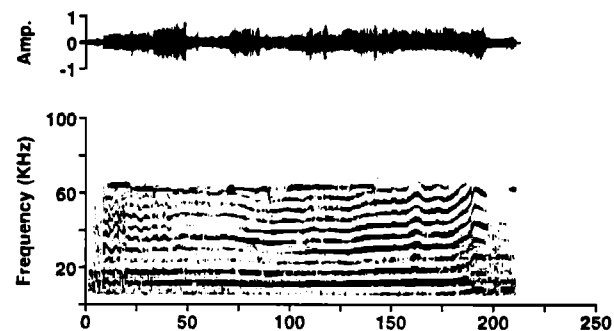
b. QCfI-pUFM. The mean duration (122.6 ± 44.8 ms; $n=7$) of this composite is not significantly different from that of QCfI-pDFM. The spectrogram of this composite appears as a mirror image of QCfI-pDFM in that it shows a 20% upward modulation at the termination of the QCfI-like component [Fig. 11(b)]. This terminal portion comprises the pUFM subsyllable. pUFM is about 18 ms long and is considered as a subsyllable because it is emitted only in combination. Its parametric boundaries show little or no overlap with those of bUFM. The mean terminal frequency is about 1 kHz higher than the initial frequency, although the peak frequency is over 2 kHz above the initial frequency.

c. QCfI-bUFM. This composite is emitted quite frequently so that 19 acoustically uncluttered examples were available for quantitative analyses [Fig. 11(c)]. The total du-

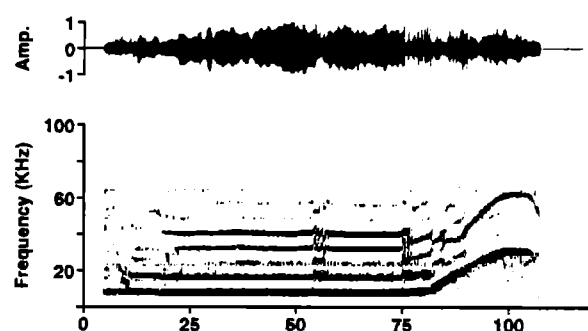
A: QCfI - paraboloid DFM (QCfI-pDFM)



B: QCfI - paraboloid UFM (QCfI-pUFM)



C: QCfI - bUFM



D: Gliding DFM - QCfI (gDFM-QCfI)

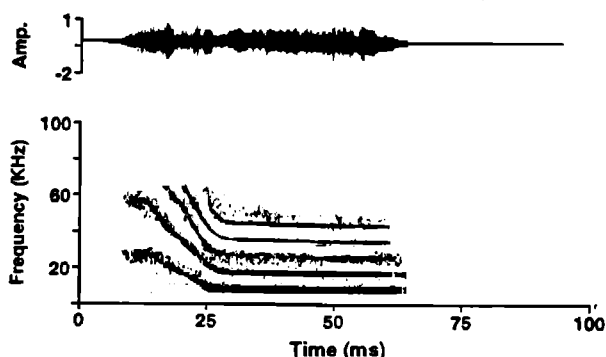


FIG. 11. (a) and (b) Sound envelope patterns and spectrograms of composites containing combinations of a CF component followed by an FM subsyllable. (c) CF-FM composite consisting of two simple syllables. (d) Sound envelope pattern and spectrogram of a composite consisting of a FM subsyllable and QCfI. Simple syllables in the composites are indicated only by their abbreviations.

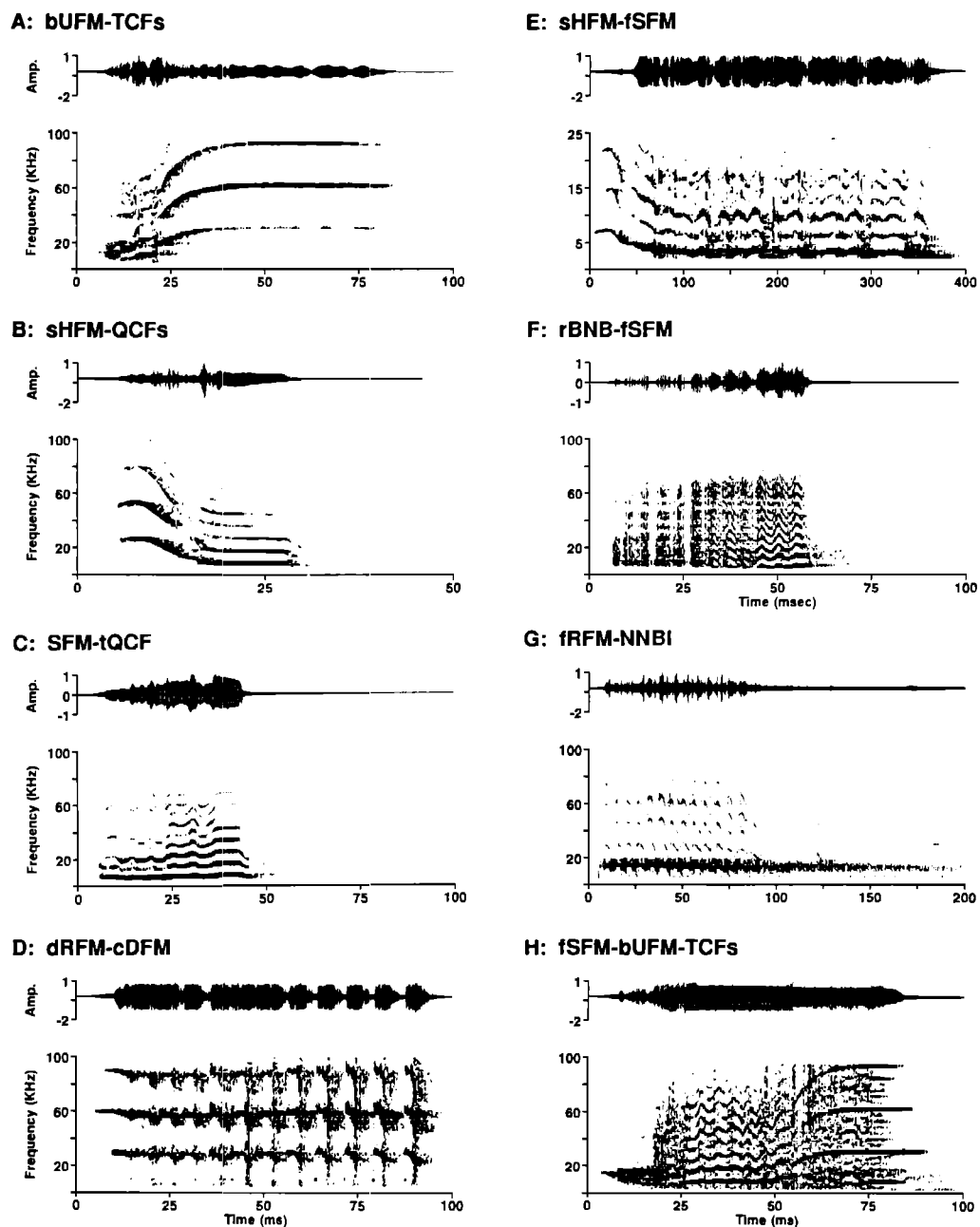


FIG. 12. (a)–(g) Sound envelope patterns and spectrograms of composites containing two components, each of which corresponds to a simple syllable. (h) Sound envelope pattern and spectrogram of an example of a composite containing three components. The fSFM and bUFM-TCFs components of this composite overlap from 55 to approximately 85 ms.

ration of this composite ranges from 79 to 340 ms. This large variation in duration is largely due to the QCFL component, which as a simple syllable also shows a great degree of variation in duration. The ascending rate of the bUFM component is about half that of the simple syllable form of bUFM. The mean terminal frequency in the bUFM in this combination is also lower than the peak frequency because of the inverted “U-like” shape of bUFM present in some of these composites. The bUFM component, therefore, is somewhat modified from the simple syllable form of bUFM and may represent one extreme of graded modifications of bUFM.

2. FM-CF combinations

FM-CF combinations are the most frequent types of combinations found in composites. This category consists of five types: gDFM-QCFL, bUFM-TCFs, fSFM-QCFs, fSFM-tQCF, and sHFM-QCFs. Of these, gDFM-QCFL is the only one containing a subsyllable, namely the gliding DFM (gDFM). The other composites are combinations of simple syllables. The construction of each composite is further described in terms of the parameters of its components.

a. gDFM-QCFL This composite has a QCFL-like component preceded by a downward hyperbolic glide (gDFM)

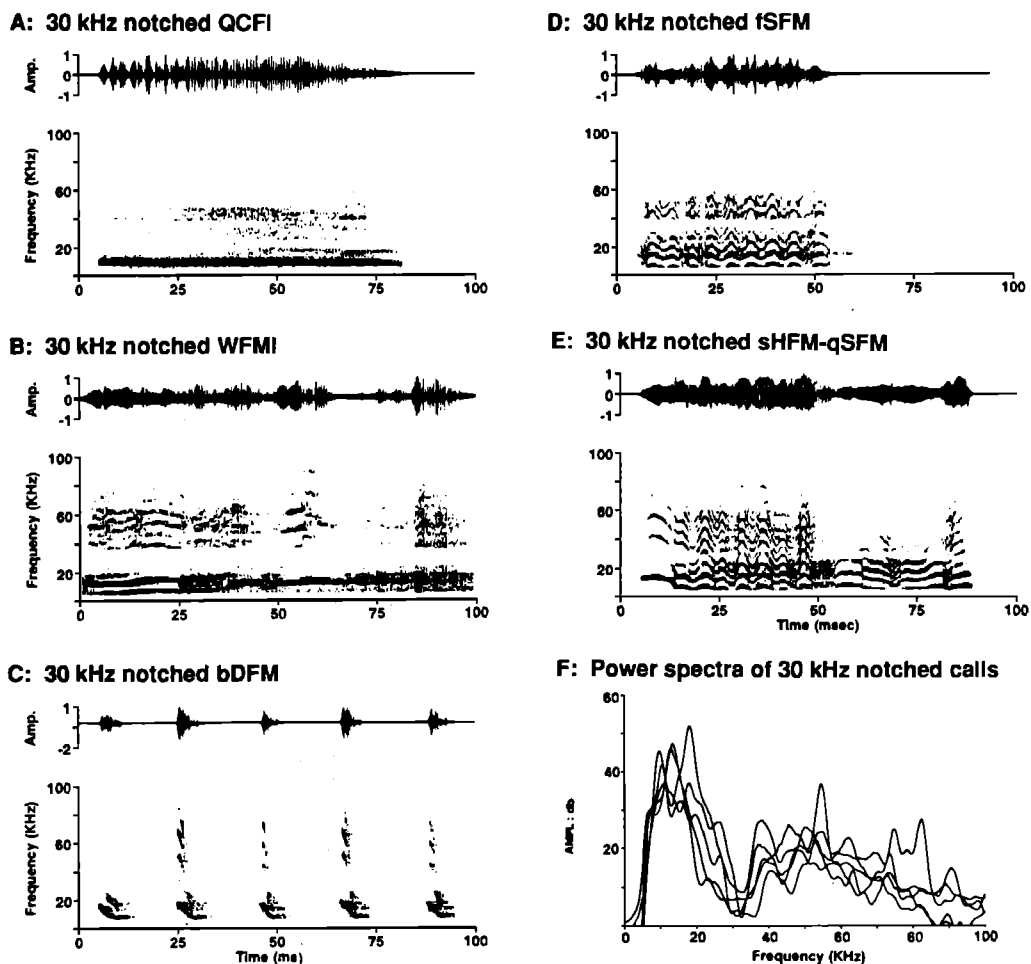


FIG. 13. (a) Sound envelop patterns and spectrograms of examples of simple syllables and composites with a missing band of energy (spectral notch) in the 30-kHz region. (b) Overlaid power spectra of the same five syllables.

from an initial frequency of about 20 to approximately 8 kHz in the fundamental [Fig. 11(d)]. Since the downward glide component is not emitted independently, it is regarded as a subsyllable. The downward glide averaged 11 ms, which gave a mean rate of downsweep of 1 kHz per ms. This rate of downward glide matches most closely to that of bDFM, although the latter is always emitted as a train of much shorter syllables. The mean overall duration of this composite is 75.2 ± 12.3 ms ($n = 12$). The fundamental is the predominant frequency in this relatively uncommon composite.

b. bUFM-TCFs. This composite starts with an upward FM (bUFM) and continues as a long plateau, which corresponds to a “TCFs-like” component [Fig. 12(a)]. To verify the presence of bUFM and TCFs components in this composite, we used several statistical tests for different parameters. Bimodality in the statistical distribution of the duration of the downward-sweeping/plateau portions in bUFM-TCFs and the independent existence of TCFs [see Fig. 3(c)] with a duration similar to the plateau portion of this composite were strong clues of its composition. Also, the duration of the TCFs component, although quite variable, roughly fitted a normal distribution. The bUFM component may be regarded as one extreme of a graded modification of bUFM since the spectrum of the bUFM component does not show the small dip at the terminal portion of the simple syllable form of

bUFM. Also, the mean duration of this composite is about 35 ms ($n = 9$), which is more than twice the mean duration of the consistent portion of bUFM.

c. fSFM-QCFs. This is a commonly emitted ($n = 28$) composite with a relatively variable pattern of the quasi-CF component. The QCFs component in this composite is always shorter than the fSFM component. The mean overall duration of this composite [second syllable in a phrase shown in Fig. 14(a)] is 90 ms with the variation ranging from a low of 44 ms and high of 128 ms. The fSFM component makes up about three fourths of this length and shows a coefficient of variation that is approximately half that of the QCFs component.

d. sHFM-QCFs. These types of composites were nearly 30 ms ($n = 6$) long and the CF portion constituted about two-thirds of this duration, i.e., nearly 20 ms [Fig. 12(b)]. The fundamental at 8.6 ± 0.9 kHz of the QCFs portion closely matches that of the QCFs emitted independently.

e. fSFM-tQCF. The mean overall duration of fSFM-tQCF is found to be 90 ms, three-fourths of which is devoted to the fSFM component [Fig. 12(c)]. The duration of the tQCF component is relatively constant. sHFM-QCFs and fSFM-tQCF were the least commonly emitted among the different types of composites.

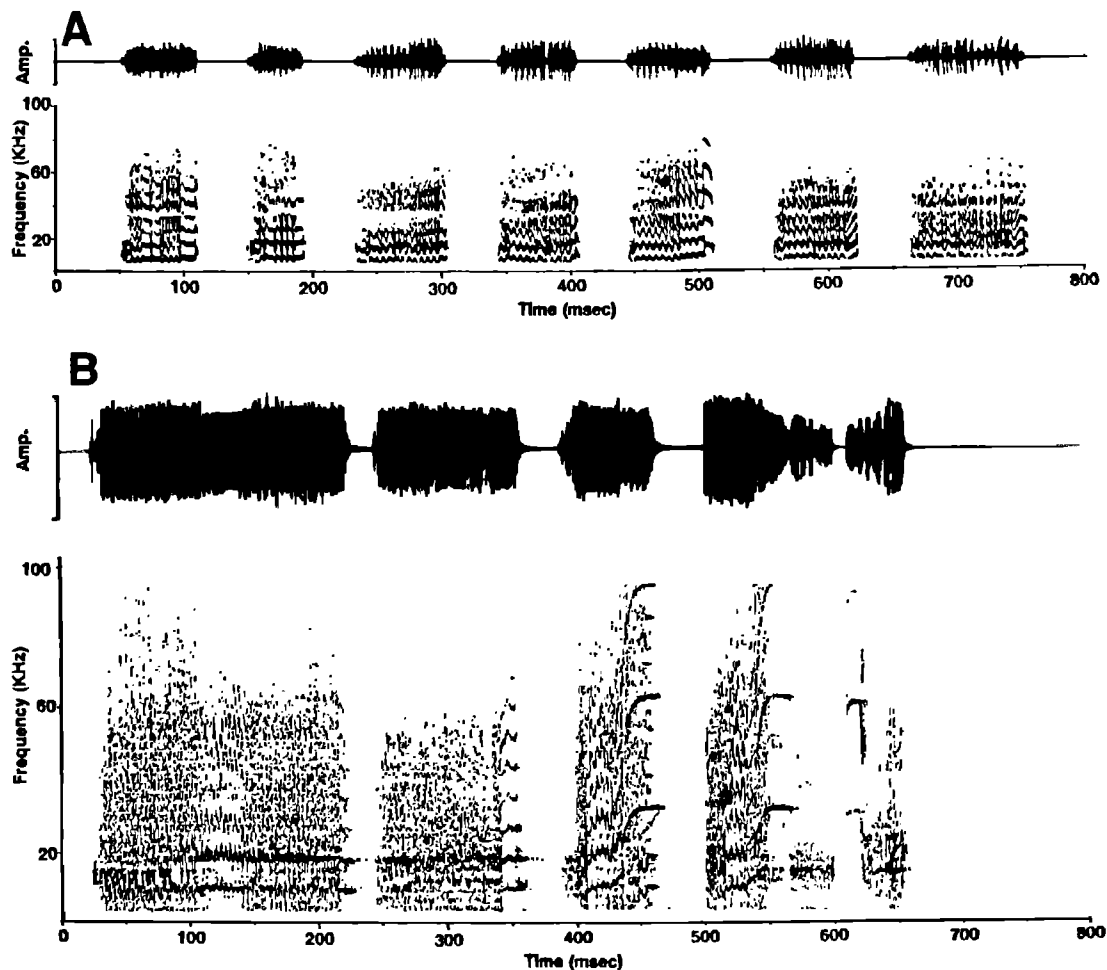


FIG. 14. (a) Sound envelop patterns and spectrograms of syllables within a phrase emitted by one bat. Note the variations in the terminal phase of a succession of fFSM and qFSM syllables in a phrase. (b) Sound envelop patterns and spectrograms of a complex phrase consisting of a sequence of simple syllables and composites emitted by another bat.

3. FM-FM combinations

We observed three types of FM-FM combinations in composites. Based on the similarity of their components to the previously defined simple syllables, the FM-FM composites are abbreviated as dRFM-cDFM, fFSM-bUFM, and sHFM-fFSM.

a. dRFM-cDFM. This composite may be easily misclassified as a cDFM alone, because cDFM is normally emitted as a train of closely spaced syllables [Fig. 12(d)]. Also, the fundamental frequency and energy distribution over the harmonics of cDFM closely matches that of dRFM so that a transition from one to the other is not apparent at first glance. A close examination, however, reveals a clear combination of two simple syllables. In the composite, dRFM is generally shorter than its simple syllabic form and consists of two or three ripples that are followed by a train of cDFM's.

b. fFSM-bUFM. This is the most commonly emitted FM-FM composite. Both the fFSM and bUFM components were quite characteristic of the simple fFSM and bUFM emitted independently. This composite is not shown separately but is included in its trisyllabic fFSM-bUFM-TCFs form (see below). The overall mean duration of this combination is about 50 ms with a wide range of variation, from 19

to 138 ms ($n=38$). Of this, over two-thirds is generally devoted to the fFSM component.

c. sHFM-fFSM. This is regarded as putative composite type because of a lack of sufficient examples for its statistical characterization [Fig. 12(e)]. Both examples of this composite type are approximately 95 ms long, although the maximum frequency modulation of harmonics of sHFM varies from 34% to 63%.

4. NB-FM combinations

a. rBNB-fFSM. This composite [Fig. 12(f)] may be easily misclassified as a fFSM, since several examples of fFSM show an intrinsic noisiness. Discriminant analysis, however, helped to identify two types of noisiness in fFSM. The spectrograms of some fFSM syllables show a background noisiness throughout, whereas other show a distinct transition from a broadband noisy component to a clean fFSM. Syllables showing the latter transition were reclassified as BNB-fFSM composites as the rBNB component can be clearly distinguished and always precedes the fFSM components alone. The duration of this composite matches that of fFSM and the rBNB components and like rBNB and fFSM, typically exhibits pronounced amplitude modulations.

5. FM-NB combinations

a. fRFM-NNBI. The fRFM-NNBI is a relatively long composite with an overall mean duration of about 200 ms, more than half of which is made up of a tail of a NNBI-like component [Fig. 12(g)]. In our *a priori* classification scheme, the fRFM component was included in the fFSM category. However, statistical analysis of various parameters showed several examples to deviate from the median at the 1σ or 2σ levels and multivariate discriminant analysis misclassified several examples in this category. This prompted a dissociation of a previously large heterogeneous fFSM group into two additional types of syllables, namely the simple fRFM and fRFM-NNBI. The duration of the fRFM component in fRFM-NNBI is more or less fixed, whereas the NNBI component itself can be longer than some of the short fRFM-NNBI composites. The fRFM component contains three to five harmonics which extend above the bandwidth of the NNBI component.

6. FM-FM-CF combinations

a. fFSM-bUFM-TCFs. This multicomponent composite consists of three simple syllables combined into one composite [Fig. 12(h)]. Usually the bUFM-TCFs sequence follows the fFSM component, although in at least four examples, the fFSM component continued for several milliseconds after the initiation of the bUFM-TCFs sequence. In this case, the fFSM component itself terminates in a QCFs-like segment during the TCFs phase of the composite. The overall syllable duration ranges from 49 to 104 ms and the duration of the bUFM and TCFs components range from 4 to 22 and 2 to 38 ms, respectively.

7. Spectral modification of syllables

Mustached bats can introduce a spectral notch or anti-resonance in the 30-kHz region of a simple syllable or a composite. Several examples of different syllables for this type of spectral filtering are provided in Fig. 13. Our recordings suggest that this notch can be introduced voluntarily within almost any syllable. Thus, examples of monosyllabic calls shown with a notch were also observed without the notch (see Figs. 3 to 6). The exact location and width of this notch may vary by up to 5 kHz, depending upon the syllable type being modified or other physical variables associated with a vocalization.

8. Phrases

Phrases can be based upon modifications of one class of syllable types, e.g., SFM, or consist of a combination of entirely different types of syllables. One of the most interesting phrases recorded was a series of 5 fFSM/qFSM variants, which were very similar to each other except for a small though distinct modification of the terminal phase [Fig. 14(a)]. Notice the consistent silent intervals between different syllables within a phrase. Another sequence of syllables in a phrase is illustrated in Fig. 14(b) to show that a phrase may consist of both simple syllables and composites. Both these uncluttered phrases recorded from two or three bats

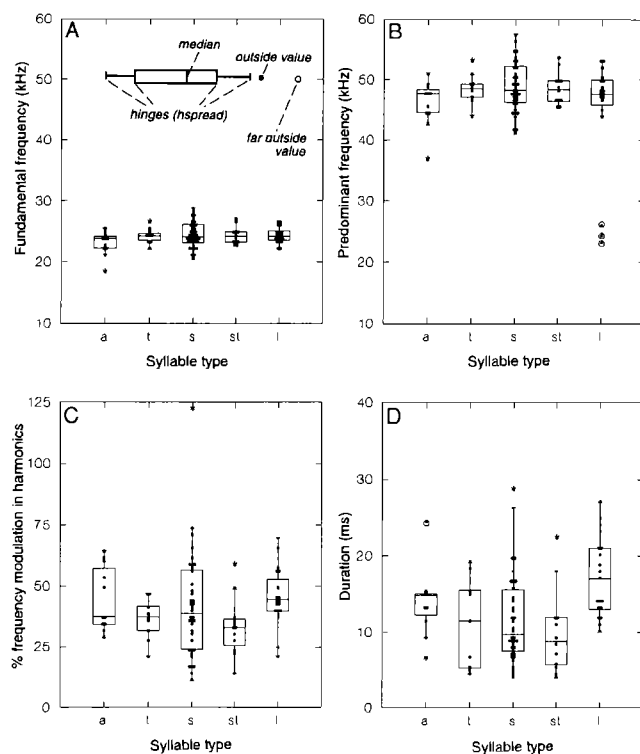


FIG. 15. Jittered density and box plots to show the distribution and range, respectively, of (a) the fundamentals, (b) predominant frequencies, (c) percent frequency modulation of the harmonics, and (d) syllable duration, in bUFM, and in the corresponding parameters of the bUFM component in several composites. The large overlap of the distributions of similar parameters in bUFM and the bUFM component in different composites is evidence of “phoneticlike” syntax (see Snowdon, 1982) for construction of composites. *a*=bUFM alone; *t*=bUFM-TCFs; *s*=bUFM-TCFs; *st*=fFSM-bUFM-TCFs; *l*=QCFI-bUFM. See Fig. 7 for additional explanation of the plots.

placed in a small cage illustrate the variety of sound combinations used for acoustic communication in mustached bats.

9. Syntax and transition analysis

As is evident from the previous description, composites represent structural combinations of simple syllables. To show this statistically, we used mid-range box plots to compare the overall range of several parameters of simple syllables with the corresponding components in a composite. The variation in four parameters of bUFM when emitted as a simple syllable and as a component of several composites is shown in the form of jittered density plots overlaid on box plots showing the mid range of each parameter [Fig. 15(a) to (d)]. This simple syllable shows no significant difference in its mean of the fundamental and predominant frequencies, the normalized frequency modulation and duration within different combinations. All combinations, however, do show a relatively large range of normal variation of the different parameters. Similar results were also obtained for fFSM, which is also a common component in several composites. Only the duration of the fFSM component within fFSM-TCFs and the tricomponent fFSM-bUFM-TCFs is significantly smaller than in the simple syllabic form of fFSM. In general, the majority of parameters of the components within

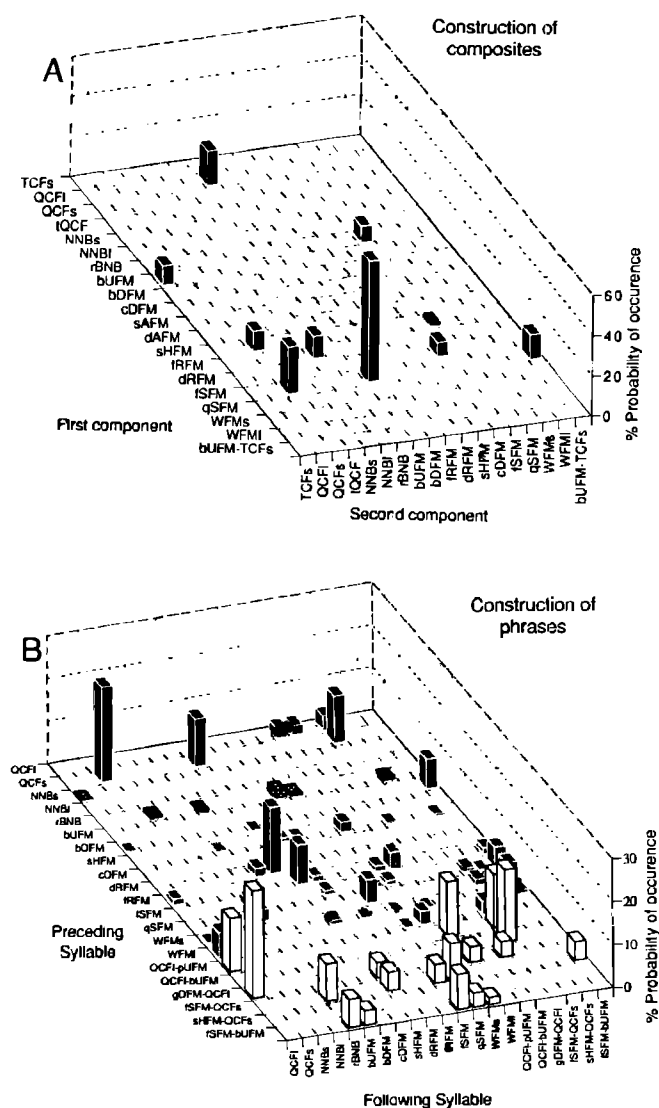


FIG. 16. (a) Three-dimensional bar chart showing the probability of production of different types of composites. The data are normalized for recordings made over a period of one hour from 65 bats in a colony. (b) Three-dimensional bar chart of a transition analysis consisting of dissimilar syllables pairs to show the probabilities with which one syllable follows another. The first syllable in the pair is shown on the left-hand side of the horizontal matrix of syllable pairs. Columns for syllable pairs in which the preceding syllable is (i) CF type are shown as solid black, (ii) NB type are cross hatched, (iii) FM type are stippled, and (iv) composites are shown as solid white.

eleven composites are statistically similar to those of the simple syllables emitted independently. Therefore, these composites can be regarded as combinations of simple syllables or simple syllable-like components. Figure 16(a) shows the construction and relative rates of vocalization of different types of composites observed in a sample analyzed using RTS. Of the 342 possible disyllabic combinations in composites, however, less than 15 have been recorded so far, suggesting the presence of strong constraints on the use of simple syllables as components of composites.

Transition analysis was performed to identify another form of syntax, namely, the associations between sequential syllable pairs, i.e., syllables in a phrase. Syllables were considered to be paired if the silent interval between two syllables was less than the combined duration of the two syl-

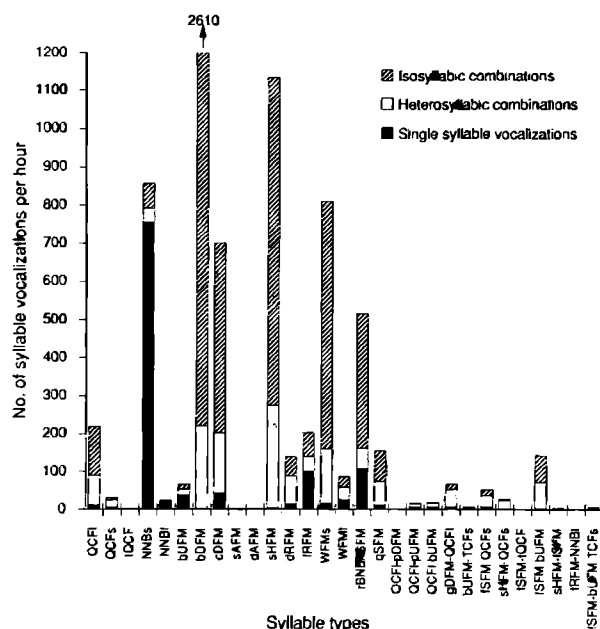


FIG. 17. Stacked histograms showing the rate of production of single syllables, the total number of paired heterosyllabic combinations in a phrase, and paired isosyllabic combinations. bDFM, sDFM, and WFMs are virtually never vocalized singly and cDFM is emitted as a single syllable for <10% of its vocalizations. These data were obtained from a colony of 65 bats.

lables surrounding the silent interval. The results are summarized in three dimensions, where the frequency of sequential transitions between any two syllables are shown as columns on a base representing the transition matrix [Fig. 16(b)]. Combinations of repeated syllables of the same type (isosyllables) normally lying on the diagonal have been omitted for purposes of clarity.

Transition analysis shows that heterosyllabic combinations occur for less than 30% of the total emissions of a syllable type. In other words, syllables are generally emitted either in isolation or as repetitions in a train. Of the ones that are paired within a phrase, composites are more frequently paired with after a simple syllable rather than a composite. Thus gDFM-QCFI most frequently precedes QCFI, although occasionally it does follow QCFI-bUFM. Two exceptions to this are the QCFI-pUFM and QCFI-bUFM to gDFM-QCFI transitions; interestingly, the composites associated with these transitions consist of a QCFI combined with a subsyllable. Other common transitions include QCFs to NNBS, dRFM to cDFM, and QCFs to gDFM-QCFI. On the whole, nearly all syllables show transitions to or from another syllable, although the relative frequency of transition for several syllables is small. However, it is important to note that of the 1056 possible heterosyllabic pairs, less than 70 seem to be actually used in a phrase.

10. Rate of syllable pairing and production

We analyzed a sample of over 3000 syllables to estimate the relative rates of syllable pairing and absolute numbers of syllable emissions in 1 h (Fig. 17). The rate of emission of different types of syllables were measured by counting syllables identified on the basis of their spectrograms using RTS. These data are pooled from three separate sound re-

cording sessions from the colony of bats at different times of the day and night. TCFs is not included in this analysis as this was difficult to identify within the clutter of echolocation sounds emitted by conspecifics in the colony. For the same reason, results of other pulse CF-like syllables, i.e., sAFM, dAFM, and cDFM are probably underestimates of their total rate of production.

A stacked histogram is used to show the frequency with which syllables are emitted singly, as part of a train (isosyllabic sequence) and in a phrase (heterosyllabic sequence). NNBS shows a nearly 90% probability of being emitted alone and is vocalized singly more frequently than any other syllable. Among others, syllables which are vocalized very frequently also show a high probability of being emitted as a train. bDFM is the most commonly emitted syllable, but is virtually never emitted as a single syllable and has a >90% probability of being emitted in a train. NNBI, sAFM, dAFM, and QCFL-pDFM are always emitted independently, but these were infrequently encountered in the sample, while fSFM-tQCF and fRFM-NNBI were not emitted at all. fSFM is commonly emitted by bats in both the flight room colony as well as by bats placed in a small cage. Additional measurements at specific times of the 24-h period can give some idea of the correlation of calls with the behavioral state or activity of the bats.

III. DISCUSSION

A. Taxonomy of communication sounds

The communication sounds of animals have been described and classified according to the behavioral repertoires that they may elicit (Maurus and Ploog, 1984), and generally named in an anthropocentric manner, i.e., on the basis of how they sound to humans (Tables VII and VIII). This method of classification and naming can lead to confusion in defining calls since "similar sounding" calls may be pooled together even though they are spectrally different and relate to subtly different behaviors (Gautier and Gautier-Hion, 1982). Furthermore, extremes of graded variants of the same call may be classified as two calls because of different functions within overlapping behavioral repertoires. This method of categorization also makes it difficult to equate similar sounds of different animal species. Thus a short squawk may consist of a CF type of syllable or a sinusoidal FM (see Table VII). Similarly, different types of noise bursts have all been defined as barks and a fSFM, a dRFM, and a cDFM have all been described as a "trill" sound. Alternatively, syllables of the same type, which contain a common SFM pattern are given quite different names such as whine, squawk, or squeak.

One approach for resolving this issue is to examine how the elements of other sensory signals are defined. Visual signals can be decomposed into a mixture of specific colors, forms, and motion and classified accordingly. Chemical signals are characterized and classified on the basis of their molecular constitution. Similarly, acoustic signals can also be classified on the basis of physical parameters of their frequency components. This provides a stable classification scheme and facilitates further descriptions of acoustic signals

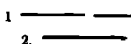
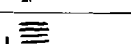
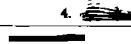
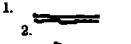
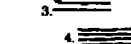
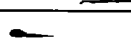
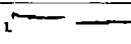
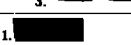
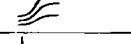
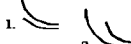
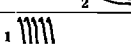
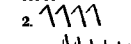
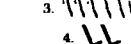
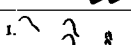
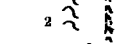
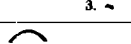
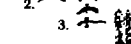
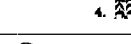
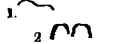
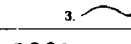
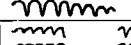
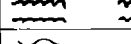
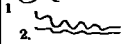
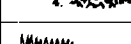
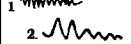
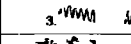
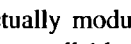
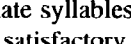
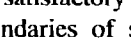
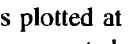
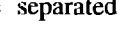
based on their biological meaning. A classification based primarily on the meaning of acoustic signals, however, is unlikely to be stable since behavioral studies involve long-term research and the results are subject to reinterpretations based on new data. On the other hand, physically defined calls are independent of the behavioral meaning and a classification based on physical parameters is unaffected by our interpretations of the meaning of calls. For our analysis of the calls of the mustached bat, therefore, we classified them purely on the basis of their physical structure. Since all animal sounds including speech sounds consist of combinations of three basic acoustic patterns or elements, i.e., constant frequency (CF), frequency modulations (FM), and noise bursts (NB) (Suga, 1971, 1992), we have classified and named the communication sounds according to their spectral composition, and the geometric patterns of FM. Our hierarchical scheme of stepwise classification of the spectral patterns can be expanded to include any new sounds observed in the mustached bat or any other species (Table VII). Our results show that mustached bats emit a rich variety of simple syllables and can also combine the simple syllables and subsyllables to create composites. The behavioral significance of some sounds with a similar acoustic structure to those reported here is already known. For example, a "warble" emitted by a harem male on return to a harem female in his roosting site in *Carollia perspicillata* (Porter, 1979) appears to be a modification of the WFMI call emitted by mustached bats.

B. Structure and classification of calls

Classifications of sounds on the basis of their physical properties can provide important clues about the communicative potential of the sender and the perceptual abilities of the listener, and also provide a reference database for future behavioral and neurophysiological studies of acoustic communication. The grouping of the bats' calls into different types of simple syllables was quite obvious in most cases where the predominant call feature corresponded to a basic sound pattern, such as in the QCFL, NNBI, and fSFM. The physical structure of syllables in the mustached bats' calls is very similar to that observed in the calls of several other bat species (see Tables VII and VIII). Several syllables, e.g., fRFM, fSFM, rBNB, and gDFM-QCFL, when tape recorded and played back at slow speed also become spectrally equivalent to the calls of many non-bat species (Rowell and Hinde, 1962; Boinski, 1991). Some syllables such as cDFM are found also in the notes of the song repertoires of birds and the humpback whale, while other patterns, e.g., bUFM, are present as a temporally reversed sequence of frequency modulations in the calls of other species (Marler and Pickert, 1984; Payne and McVay, 1971).

Although mustached bats can emit stereotypic echolocation pulses, the physical structure of their syllables show a large degree of inherent variation (see Figs. 8 and 9). As a result, syllable types tend to intergrade if defined only on the basis of any one parameter. An effective separation can be achieved, however, if syllables are defined on the basis of multiple parameters. Some of these parameters covary and may play an important role in constraining the perception of sounds under adverse signal to noise conditions. In order to

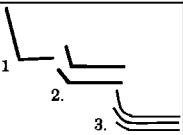
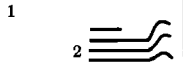
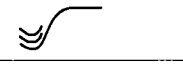
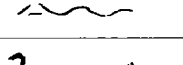
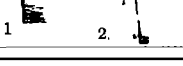
TABLE VII. Scheme for naming simple syllables in bats applied to examples of communication sounds reported in other species.

NOMENCLATURE BASED UPON THE PHYSICAL STRUCTURE OF SYLLABLES			SCHEMATIZED SONAGRAMS	GIVEN SOUND NAME/S	SPECIES	REFERENCES
Constant frequency (CF) sounds	True CF (TCFs)	short, TCF (TCFs)	1.  2. 	1. sustained or wavering tone 2. whistle	1. humpback whale 2. white-crowned sparrow	1. Payne & McVay, '71; p. 591. 2. Margoliash, '83; p. 1041.
	Quasi CF (QCF)	short, QCF (QCFs)	1.  2.  3.  4.  5. 	1. short squawk 2. fish sound 3. (separation vocalization) 4. audible squeak 5. audible squeak	1. <i>Myotis lucifugus</i> 2. Dying gurnard 3. rhesus monkey 4. water shrew 5. musk shrew	1. Fenton, '85; p. 107. 2. Pluh, '70, p. 159, 162. 3. Sales & Pye, '74; p. 384. 4. Sales & Pye, '74; Plate XIV. 5. Sales & Pye, '74; Plate XIV.
		long, QCF (QCFI)	1.  2.  3.  4.  5. 	1. arrow phrase 2. long low-frequency ultrasonic call 3. fish sound 4a whine 4b long squawk	1. <i>Cebus nigritatus</i> 2. laboratory rat 3. grubby longhorn sculpin 4a <i>Myotis lucifugus</i> 4b <i>Carollia perspicillata</i>	1. Robinson, '82; p. 98. 2. Sales & Pye, '74; p. 174. 3. Pluh, '70; p. 159, 160. 4. Fenton, '85; (a) p. 107, (b) p. 108
Noise bursts (NB)	Narrowband NB (NNB)	short, NNB (NNBs)		bark	<i>Saccopteryx bilineata</i>	Bradbury & Emmons '74; p. 157.
		long, NNB (NNBI)	1.  2.  3. 	1. fee bee song 2. narrow-band ultrasonic call 3. buzz	1. black-capped chickadee 2. 3-day-old hamster 3. white-crowned sparrow	1. Ratcliffe & Weisman, '92; p. 214 2. Sales & Pye, '74; p. 161. 3. Margoliash, '83; p. 1041.
	Broadband NB (BNB)	rectangular BNB (rBNB)	1.  2.  3.  4.  5. 	1. long bark 2. broad-band call 3. low-freq. 'creek' 4. screech 5. long call	1. <i>Myotis lucifugus</i> 2. 1-day-old hamster 3. bottlenose dolphin 4. <i>P. poliocephalus</i> 5. <i>P. poliocephalus</i>	1. Fenton, '77; p. 1163. 2. Sales & Pye, '74; p. 161. 3. Sales & Pye, '74; Plate XII. 4. Fenton, '85; p. 108; 5. Fenton, '85; p. 109.
		trapezoidal BNB (tBNB) - (5.)				
Frequency Modulated (FM) sounds	Upward FM (UFM)	bent UFM (bUFM)		harsh scream	rhesus monkey	Rowell and Hinde, '82; p. 285.
	Downward FM (DFM)	bent DFM (bDFM)	1.  2. 	1. female contact 2. ang squeak	1. <i>Myotis lucifugus</i> 2. <i>Myotis lucifugus</i>	1. Fenton, '85; p. 109. 2. Thomas et al., '79; p. 143.
		checked DFM (cDFM)	1.  2.  3.  4.  5. 	1a chatter 1b hook notes 2. harsh chirrup 3. trill 4. back checks	1a. Squirrel monkey 1b. <i>S. bilineata</i> 2. rock hyrax 3. white-crowned sparrow 4. <i>Carollia perspicillata</i>	1a. Jurgens, '82; p. 54. 1b. Bradbury & Emmons '74; p. 161 2. Foerster, '77; p. 206. 3. Margoliash, '83; p. 1041. 4. Fenton, '85; p. 108.
		single HFM (sHFM)	1.  2.  3.  4.  5. 	1. Smooth chuck. 2. (panic call) 3. chirp	1. squirrel monkey 2. young pika 3. <i>Bufo boreas</i>	1. Boinaki, '91; p. 94. 2. Conner & Whitworth, '85; p. 759 3. Bogert, '60; p. 176.
	Arched FM (AFM)	single AFM (sAFM)	1.  2.  3.  4.  5. 	1. ultrasound with rapid freq. changes 2. short call 3a (isolation call) 3b (isolation (I) call) 4. HP1	1. male laboratory rat 2. young pika 3a. domestic cat 3b. <i>Myotis lucifugus</i> 4. human infant	1. Sales & Pye, '74; p. 174. 2. Conner & Whitworth, '85; p. 759 3a. Fenton, '77; p. 1154. 3b. Buchwald et al., '88; p. 124. 4. Bryan & Newman, '88; p. 422.
		double AFM (dAFM)	1.  2.  3. 	1. peep 2. rapid frequency fluctuation 3. whistle	1. squirrel monkey 2. laboratory rat 3. <i>Turnipus truncatus</i>	1. Boinaki, '91; p. 94. 2. Sales & Pye, '74; p. 186. 3. Sales & Pye, '74; p. 207.
	Rippled FM (RFM)	fixed RFM (fRFM)		twitter	squirrel monkey	Boinaki, '91; p. 94.
		descending RFM (dRFM)		descending RFM	mustached bat	Kanwal et al, this manuscript.
	Sinusoidal FM (SFM)	fixed SFM (fSFM)	1.  2.  3. 4.	1. sine wave call 2. whine 3. short squawk 4. audible squeak	1. <i>Myotis lucifugus</i> 2. <i>Carollia perspicillata</i> 3. <i>Myotis lucifugus</i> 4. Sicily Isles shrew	1. Thomas et al., '79; p. 143 2. Porter, '79; p. 3. 3. Thomas et al., '79, p. 139. 4. Sales & Pye, '74; Plate XII.
		toothed SFM (tSFM)	1. 2. 3.	1a trill 1b isolation trill 2. warble 3. two twitters	1a. <i>C. perspicillata</i> 1b. <i>P. poliocephalus</i> 2. <i>C. perspicillata</i> 3. squirrel monkey	1. Fenton, '85; (a) p. 108, (b) p. 109 2. Fenton, '85; p. 108. 3. Newman & Wollberg, '73; p. 290
	Wrinkled FM (WFM)	short, WFM (WFMs)		1. LF1.	human infant	Bryan & Newman, '88; p. 419.
		long, WFM (WFMI)	1. 2.	1. LP3, HP3 2. warning cry	1. human infant 2. <i>Rana clamitans</i>	1. Bryan & Newman, '88; p. 422, 429. 2. Bogert, '60; p. 176.

see how many parameters are actually modulated independently, we collapsed the multivariate syllables onto three dimensions and found a reasonably satisfactory distinction between the multidimensional boundaries of syllable types. According to the bivariate ellipses plotted at the 75% probability level, most syllables are separated completely or

showed only minor overlap, e.g., bUFM/cDFM, and sAFM/dAFM syllable clusters, within the three-dimensional space. Two exceptions are the tightly grouped bDFM and qSFM syllables, which are interposed between the domains of fRFM and fSFM and exhibit a substantial overlap with them. On the basis of this scatter plot, one may consider qSFM as

TABLE VIII. Scheme for naming composites in bats applied to examples of communication sounds in other species.

	NOMENCLATURE BASED UPON THE PHYSICAL COMPOSITION	SCHEMATIZED SONAGRAMS	GIVEN SOUND NAME/S	SPECIES	REFERENCES
CF/FM COMPOSITES	gliding Downward FM-long, Quasi CF (gDFM-QCFI)		1. FMGE 2. isolation trill 3. FM glide	1. <i>Leptonycteris</i> 2. <i>Antrozus pallidus</i> 3. <i>Carollia perspicillata</i>	1. Gould, '77; p. 254. 2. Brown, '76; p. 36. 3. Porter, '79; p. 3.
	long, Quasi CF - paraboloid Upward FM (QCFI-pUFM)		1. Roman isolation peep 2. (thwart)	1. white-crowned sparrow 2. budgerigar	1. Newman, '85b; p. 319. 2. Dooling et al., '87; p.371.
	bUFM-TCFs		sigmoidal freq. modulation	<i>Saccopteryx bilineata</i>	Bradbury & Emmons '74; p.160.
	QCFs/fSFM		call showing step and freq. modulations	<i>Lagurus lagurus</i>	Sales & Pye, '74; p. 190
	sHFM-QCFs		1. yap with a prominent cackle component, 2. chuck	1. squirrel monkey 2. squirrel monkey	1. Newman, '85; p. 108. 2. Ploog et al., '75; p. 250.

a graded variant of fSFM since the only difference between their sound spectra is the inclusion of quasi-CF components at different locations within the SFM pattern. bDFM, however, is spectrally distinct from both fRFM and fSFM, although the parameters used in this analysis do not provide adequate separation on the basis of the first three principal components.

In the MDS configuration, where additional parameters, such as maximum FM depth, delay between two consecutive FM sweeps and predominant bandwidth, are taken into account, bDFM is placed diagonally across from fSFM and fRFM syllable types. Syllables, e.g., TCFs and dAFM, that may sound the same to the human ear when played back slowly are also separated, although barely, in the MDS configuration. As expected, syllables with different types of the basic sound elements are the most widely separated. Echolocation pulses, which may be considered as composites containing two components (CF and FM), are placed in the center of the plot.

An outstanding feature of calls in bats is the variety of simple syllables and composites emitted by conspecifics in the same colony. This is in contrast to the simple repeating sounds of frogs and toads (Wells and Schwartz, 1984) and the stereotypic song sequences of some birds (Marler and Pickert, 1984). Our studies show that the composition and variation in the call structure of mustached bats is among the richest in the sounds produced by animals. Only primate species including the squirrel monkey and macaques produce such a rich repertoire of vocalizations (Sutton, 1979). However, an objective structural analysis of the parametric boundaries of the natural variants of communication sounds in these species is lacking. This variation presumably contains important information such as the identity of the emitter (Suga, 1978) and the behavioral context in which a syllable variant is emitted. The structural variation also suggests that the animal is capable of generalizing variants of syllable types to have a common meaning. Interestingly, not all syllables show the same degree of overall variation. Some of the tightly clustered syllables, e.g., the bDFM and WFM, may correspond to warning or alarm calls, where it is critical

to avoid ambiguity in the message and where the identity of the emitter is unimportant. Behavioral studies, however, are necessary to test this hypothesis.

C. Mechanisms of sound production

What does our analysis of call structure tell us about the mechanisms of sound production in bats? Several interesting facts emerge. Examination of the sound spectrogram of calls emitted by the mustached bat suggests that mechanisms of sound production in this species are conventionally mammalian. That is, they show clear harmonics of a single fundamental frequency, and the intensity of higher harmonics generally decreases in a graded fashion. The spectrum appears to be further shaped by the vocal tract, primarily in the form of reduced acoustic energy near 30 kHz (Fig. 13). All this is consistent with the idea of a single laryngeal source being in series with a supralaryngeal filter, as has already been suggested for this species and other microchiropteran bats (Griffin, 1974; Novick, 1977; Suthers, 1988). Mechanisms for the production of echolocation pulses were examined in detail in the mustached bat by Hartley and Suthers (1990). They suggested that the supralaryngeal tract comprises two separate 30 kHz antiresonances, one involving the nasal passages, and the other related to the cross-sectional area of the vocal tract. Since they examined only echolocation pulse emission, they did not determine whether these antiresonances were evident in other types of sounds. It is clear by examining our sound spectrograms that the 30-kHz notch is not always apparent. In fact, the presence or absence of the 30-kHz notch appears highly variable for most syllable types. We, therefore, speculate that the 30-kHz notch is under voluntary control. It is thus possible that the activation of this filtering mechanism during emission of a given call either influences the meaning of a call or simply reduces the effect of masking by harmonics of 30-kHz frequencies in the echolocation pulse and its echo.

We also noticed four instances of fSFM-bUFM-TCFs vocalizations that are not consistent with conventional mammalian sound production mechanisms [Fig. 12(h)]. For ap-

proximately the last 30 ms of this syllable type, there appear to be two fundamental frequencies and frequency modulation patterns. A sinusoidally modulated fundamental near 10 kHz overlaps with the bUFM and TCFs components. This overlap suggests the presence of two laryngeal generators. Dual sound generators have been described only for the avian syrinx (Greenewalt, 1968). Other types of communication sounds with two components have also been observed in several other species of bats although a clear explanation of their production mechanisms is lacking (Bradbury, 1970, 1977; Gould, 1977).

Even though the production of sound in bats has been described as conventional, the laryngeal anatomy of the bat would seem to allow other possibilities for laryngeal generators. In addition to the vocal membranes, which have been shown to be the source for generating echolocation pulses (Suthers and Fattu, 1973; Suthers, 1988), bats possess two other paired structures. These are the vocal folds and ventricular membranes (Griffin, 1974; Griffiths, 1983; Suthers, 1988). From the peculiar arrangement of the vocal folds and ventricular membranes (Griffin, 1974), it is not clear whether these function together by adducting across the midline, or if the latter have any function at all. It is thought that vocal folds are used to gate vocalizations, and thus allow a rapid onset, characteristic of echolocation pulses. We can speculate at least three possibilities for the identity of the second generator that may be tested experimentally. First, the left and right vocal membranes may conceivably oscillate at different frequencies in a manner analogous to the independent control of left and right syrinxes in birds (e.g., Nowicki and Capranica, 1986). Other possibilities are that vocal folds serve as the primary oscillator and the ventricular membranes act as a second sound generator or vice versa.

D. Syntax

Since bats frequently combine independently emitted simple syllables within composites, we have to ask the question, "what are the rules for joining simple syllables to produce composites?" Several syntactical rules can be formulated from our knowledge of the bat's repertoire of calls. Rules for these types of combinations in communication sounds of primates have been referred to as "phoneticlike" syntax (Snowdon, 1982) and in bird song as syllabic syntax (Marler and Peters, 1989), although in the latter short silent intervals are included within a syllable. The rules pertaining to the construction of composites from the simple syllables and subsyllables in the calls of the mustached bat are listed below.

(1) Simple syllables are not conjoined in any random fashion for creating composites. From our recordings of the call vocalizations, only 11 of the 19 simple syllables are used to construct composites.

(2) The bUFM component is never followed by an attached syllable whose fundamental is lower than the mean terminal frequency of the bUFM.

(3) In the dRFM-cDFM composite, the dRFM component always precedes cDFM, although the length of dRFM, i.e., the number of ripples, may vary from syllable to syllable.

(4) Those syllable types consisting of syllables that are always emitted in pairs or in a train (e.g., cDFM or WFM) are not combined with a syllable type that is always emitted singly.

(5) When syllables that are emitted naturally as a train are combined, such as in the dRFM-cDFM combination, a train of the first syllable is followed by a train of the next, resulting in a complex multisyllabic call.

(6) An fFSM component usually precedes a QCFs or a QCFs-like component.

(7) A maximum of three simple syllables may be combined to form a composite. Clear and substantiated examples of combinations of more than three components in a composite have not been observed.

Only the duration parameter of a simple syllable appears to be significantly altered when that syllable is combined within a composite, e.g., bUFM (see Fig. 11). This total duration of a syllable is probably constrained by the lung volume and respiratory rate of the animal (Suthers and Fattu, 1973) and therefore the duration of one component in a composite is significantly modified. There is no information on the normal breathing rate or vital capacity of *Pteronotus*. Our incidental measurements show that the breathing rate of hand-held or restrained bats ranges from 158 breaths/minute to 300 breaths/minute. However, actual rates may be lower and vary depending upon whether the bat is roosting or flying. We do know that although most syllables are less than 100 ms in length, they can be as long as 400 ms. This gives a minimal breathing rate of 150 breaths/minute.

The syntax for creating composites may be further constrained either by mechanisms of sound production or other rules of construction and perception of the message. These cannot be identified without functional-anatomical and behavioral studies of sound communication.

Rules governing the phrasing of simple syllables and composites in a phrase, monologue or a dialogue ("lexical-like" syntax; see Snowdon, 1982 and segmental syntax; see Marler and Peters, 1988) are more difficult to define at present because of the difficulty in separating sounds of different bats in a large colony. On the other hand, recording from a few bats in a cage may restrict the elaboration of behaviors to which syllables and higher order constructs are linked. However, lengthy dialogues were occasionally observed even under these conditions. We can, therefore, make a few generalizations from the simultaneous audio and video recordings of bats and from the transition analysis of syllable pairs. These are listed below.

1. Simple syllables are vocalized singly or in isosyllabic trains for about 70% of their occurrence.

2. The cDFM, dRFM, WFM, and bDFM syllables are rarely emitted singly and a complete call consists of a variable length train of similar syllables, although the number of syllables in each train may vary. Subsyllables, by definition, are not emitted singly and only occur in combinations in composites; in this respect they may be equated to the phonemes of human speech.

3. Simple syllables and composites may be emitted together in a sequence in a call or phrase. Composites are more

likely to be paired with a simple syllable than with a composite.

E. Acoustic communication and social behavior

Several studies in primates show that animals may marginally alter parts of a call to transmit related bits of information (Struhsaker, 1976; Green, 1975; Petersen, 1982). These studies suggest that acoustic communication is more highly evolved in animals than was previously suspected. Elegant studies by Seyfarth *et al.* (1980) have shown that vervet monkeys give different alarm calls to different predators to warn conspecifics of the source of the danger, e.g., from eagles, leopards, or snakes. Marler and co-workers reported that similar abilities are present in the domestic chicken as well (Evans and Marler, 1991). These studies, however, are exceptional examples of a careful experimental design and analysis using an appropriately selected animal model.

In most other studies of acoustic communication, sounds are simply classified on the basis of the behavior associated with that vocalization (Winter *et al.*, 1966; Dooling *et al.*, 1987). A few examples are included in Tables VII and VIII (sound names in parentheses). Before establishing intimate associations of acoustic communication with social behavior, however, it is important to know the physical characteristics and the natural structural variations in complex sounds, just as it is to know the structure of a society. This is also useful for testing whether the cognitive capacity of a species matches the variation and complexity of its vocalizations and to directly investigate the role of acoustic communication during different types of social interactions. Furthermore, in most animal species, the same vocalization may be accompanied by different gestures so that the same sound signal may be interpreted differently by the receiver. Thus it is difficult to conduct an analysis of the communicative significance or information content without having a clear understanding of the sound structure itself.

The behavioral significance of minor differences in sound structure can be studied more accurately in microchiropteran bats than in most other animals because in this species vocal signals are less likely to be complicated by non-vocal signals, e.g., visual gestures, which are quite useless in their dark habitat. Thus mustached bats may prove to be excellent models for studying the upper limit of complexity of acoustic communication in animals. Although our analysis of the sound structure of calls was extensive, it is quite likely that these bats use additional types of syllables which we have not yet recorded, e.g., those emitted during mother-baby interactions.

IV. SUMMARY

Our studies of the variety and complexity of sound structure in the mustached bat suggest that this species uses a structurally complex repertoire of sounds that is no less elaborate than that of any other mammalian species. Statistical analysis suggests that to unambiguously encode the bats' calls, perceptual discrimination of two or more of the independently varying parameters in syllables is essential. Our

characterization of syllable types provides an excellent database for designing acoustic stimuli for behavioral experiments as well as for the neurophysiology of call processing. Laboratory and field studies of the bat's behavior, however, are necessary to know the extent to which the perceptual ability and social structure of the mustached bat matches the complexity of its communication sound patterns.

ACKNOWLEDGMENTS

This research was supported in part by NIH Grants NS07057 to J. K., DC00076 to K. K. O. and DC00175 to N.S. and a "research worker abroad" grant from the Japanese Ministry of Education to S. M. We thank D. A. Chisholm for technical assistance and the people of Jamaica who helped us catch the bats and also the Jamaican Ministry of Agriculture for permitting export of mustached bats from Jamaica.

APPENDIX: LIST OF ABBREVIATIONS OF SYLLABLE TYPES

Abbreviation	Syllable name	Illustrations (figure)
TCFs	=Short, true CF	3(c)
QCFs	=Short, quasi CF	3(d1)
QCFI	=Long, quasi CF	3(e)
tQCF	=Trapezoidal, quasi CF	3(d)2
NNBs	=Short, narrow-band NB	4(a)
NNBI	=Long, narrow-band NB	4(b)
rBNB	=Rectangular, broadband NB	4(c)
bUFM	=Bent, upward FM	5(a)
bDFM	=Bent, downward FM	5(b)
cDFM	=Checked, downward FM	5(c)
sAFM	=Single, arched FM	5(d)
dAFM	=Double, arched FM	5(e)
sHFM	=Single, humped FM	5(f)
dRFM	=Downward, rippled FM	5(g)
fRFM	=Fixed, rippled FM	5(h)
fSFM	=Fixed, sinusoidal FM	6(a)
qSFM	=Quasi, sinusoidal FM	6(b)
WFMs	=Short, wrinkled FM	6(c)
WFMI	=Long, wrinkled FM	6(d)

- Balcombe, J. P. (1990). "Vocal recognition of pups by mother Mexican free-tailed bats, *Tadarida brasiliensis mexicana*," *Anim. Behav.* **39**, 960-966.
- Boinski, S. (1991). "The coordination of spatial position: a field study of the vocal behavior of adult female squirrel monkeys," *Anim. Behav.* **41**, 89-102.
- Bogert, C. M. (1960). "The influence of sound on the behavior of amphibians and reptiles," in *Animal Sounds and Communication*, edited by W. E. Lanyon and W. N. Tavolga (American Institute of Biological Sciences, Washington, DC), pp. 137-320.
- Bradbury, J. W. (1970). "Target discrimination by the echolocating bat *Vampyrus spectrum*," *J. Exp. Zool.* **173**, 23-46.
- Bradbury, J. (1977). "Social organization and communication," in *Biology of Bats*, edited by W. A. Wimsatt (Academic, New York), Vol. 3, pp. 1-73.
- Bradbury, J. W., and Emmons, L. H. (1974). "Social organization of some Trinidad bats: I. Emballonuridae," *Z. Tierpsychol.* **36**, 137-183.
- Brown, P. (1976). "Vocal communication in the pallid bat, *Antrozous pallidus*," *Z. Tierpsychol.* **41**, 34-54.
- Brown, P. E., Brown, T. W., and Grinnell, A. D. (1983). "Echolocation behavior, development, and vocal communication in the lesser bulldog bat, *Noctilio albiventris*," *Behav. Ecol. Sociobiol.* **13**, 287-298.

- Bryan, Y. E., and Newman, J. D. (1988). "Influence of infant cry structure on heart rate of the listener," in *The Physiological Control of Mammalian Vocalization*, edited by J. D. Newman (Plenum, New York), pp. 413–432, 1st ed.
- Buchwald, J. S., Shipley, C., Altafullah, I., Hinman, J., Harrison, J., and Dickerson, L. (1988). "The feline isolation call," in *The Physiological Control of Mammalian Vocalization*, edited by J. D. Newman (Plenum, New York) pp. 119–136.
- Conner, D. A., and Whitworth, M. R. (1985). "The ontogeny of vocal communication in the pika," *J. Mammal.* **66**, 756–763.
- Dooling, R. J., Park, T. J., Brown, S. D., Okanoya, K., and Soli, S. D. (1987). "Perceptual organization of acoustic stimuli by budgerigars (*Melopsittacus undulatus*): II. vocal signals," *J. Comp. Psychol.* **101**, 367–381.
- Duntelman, G. H. (1984). *Introduction of Multivariate Analysis* (Sage Publications, Beverly Hills), pp. 107–180.
- Ehret, G. (1989). "Hearing in the mouse," in *The Comparative Psychology of Audition: Perceiving Complex Sounds*, edited by R. J. Dooling and S. H. Hulse (Erlbaum, Hillsdale, NJ), pp. 3–34.
- Eisenberg, J. F. (1976). "Communication mechanisms and social integration in the black spider monkey (*Ateles fusciceps robustus*) and related species," *Smithson. Contrib. Zool.* **213**, 1–108.
- Evans, C. S., and Marler, P. (1991). "On the use of video images as social stimuli in birds: audience effects on alarm calling," *Anim. Behav.* **41**, 17–26.
- Fenton, M. B. (1977). "Variations in the social calls of little brown bats (*Myotis lucifugus*)," *Can. J. Zool.* **55**, 1151–1157.
- Fenton, M. B. (1985). *Communication in the Chiroptera* (Indiana U.P., Bloomington, IN).
- Fish, M. P., and Mowbray, W. H. (1970). "Sounds of Western North Atlantic Fishes," (John Hopkins Press, Baltimore, MD), pp. 59–61.
- Fitzpatrick, D. C., Suga, N., and Misawa, H. (1991). "Are the initial frequency-modulated components of the mustached bat's biosonar pulses important for ranging," *J. Neurophysiol.* **66**, 1951–1964.
- Fourie, P. B. (1977). "Acoustic communication in the rock hyrax, *Procavia capensis*," *Z. Tierpsychol.* **44**, 194–219.
- Fuzessery, Z. M., and Feng, A. S. (1983). "Mating call selectivity in the thalamus of the leopard frog, (*Rana p. pipiens*): Single and multiunit analyses," *J. Comp. Physiol.* **150**, 333–344.
- Gautier, J.-P. (1974). "Field and laboratory studies of the vocalizations of the talapoin monkeys (*Miopithecus talapoin*)," *Behaviour* **51**, 209–273.
- Gautier, J.-P., and Gautier-Hion, A. (1982). "Vocal communication within a group of monkeys: an analysis by biotelemetry," in *Primate communication*, edited by C. T. Snowdon, C. H. Brown, and M. R. Petersen (Cambridge U.P., Cambridge, England), pp. 5–29.
- Goodwin, R. E. (1970). "The ecology of Jamaican bats," *J. Mammal.* **51**, 571–579.
- Gould, E. (1971). "Studies of maternal-infant communication and development of vocalizations in the bats, *Myotis* and *Eptesicus*," in *Communications in Behavioral Biology* (Academic, New York), pp. 263–313.
- Gould, E. (1977). "Echolocation and communication," Special publications museum Texas Tech University, pp. 247–279.
- Green, S. (1975). "Variations of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): a field study," in *Primate Behavior* (Vol. 4), *Developments in field and laboratory research*, edited by L. A. Rosenblum (Academic, New York), pp. 1–102.
- Griffin, D. R. (1974). *Listening in the Dark: The Acoustic Orientation of Bats and Men* (Dover, New York).
- Griffiths, T. A. (1983). "Comparative laryngeal anatomy of the big brown bat, *Eptesicus fuscus*, and the mustached bat, *Pteronotus parnellii*," *Mammalia* **47**, 378–394.
- Greenewalt, C. H. (1968). *Bird Song: Acoustics and Physiology* (Smithsonian Institution Press, Washington, DC), pp. 279–247.
- Hand, D. J. (1981). *Discrimination and Classification* (Wiley, New York).
- Hartley, D. J., and Suthers, R. A. (1990). "Sonar pulse radiation and filtering in the mustached bat, *Pteronotus parnellii rubiginosus*," *J. Acoust. Soc. Am.* **87**, 2756–2772.
- Jürgens, U. (1982). "A neuroethological approach to the classification of vocalization in the squirrel monkey," in *Primate Communication*, edited by C. T. Snowdon, C. H. Brown, and M. R. Petersen (Cambridge U.P., Cambridge), pp. 50–62.
- Kroodsmas, D. E. (1977). "A re-evaluation of song development in the song sparrow," *Anim. Behav.* **25**, 390–399.
- Kruskal, J. B. (1964). "Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis," *Psychometrika* **29**, 1–25.
- Margoliash, D. (1983). "Acoustic parameters underlying the responses of son-specific neurons in the white-crowned sparrow," *J. Neurosci.* **3**, 1039–1057.
- Margoliash, D., and Fortune, E. S. (1992). "Temporal and Harmonic combination-sensitive neurons in the zebra finch's HVC," *J. Neurosci.* **12**, 4309–4326.
- Marler, P., and Pickert, R. (1984). "Species-universal microstructure in the learned song of the swamp sparrow (*Melospiza georgiana*)," *Anim. Behav.* **32**, 673–689.
- Marler, P., and Peters S. (1988). "The role of song phonology and syntax in vocal learning preferences in the song sparrow, *Melospiza melodia*," *Ethology* **77**, 125–149.
- Marler, P., and Peters, S. (1989). "Species differences in auditory responsiveness in early vocal learning," in *The Comparative Psychology of Audition: Perceiving Complex Sounds*, edited by R. J. Dooling and S. H. Hulse (Erlbaum, Hillsdale, NJ), pp. 243–273.
- Matsumura, S. (1979). "Mother-infant communication in a horseshoe bat (*Rhinolophus ferrumequinum nippon*): Development of vocalization," *J. Mammal.* **60**, 76–84.
- Matsumura, S. (1981). "Mother-infant communication in a horseshoe bat (*Rhinolophus ferrumequinum nippon*): vocal communication in three-week-old infants," *J. Mammal.* **62**, 20–28.
- Maurus, M., and Ploog, D. (1984). "Categorization of social signals as derived from quantitative analyses of communication processes," in *The Meaning of Primate Signals*, edited by R. Harre and V. Reynolds (Cambridge U.P., Cambridge), pp. 226–240.
- McLachlan, G. J. (1992). *Discriminant Analysis and Statistical Pattern Recognition* (Wiley, New York).
- Newman, J. D. (1979). "Central nervous system processing of sounds in primates," in *Neurobiology of Social Communication in Primates*, edited by H. D. Steklis and M. J. Raleigh (Academic, New York), pp. 69–131.
- Newman, J. D. (1985a). "Squirrel monkey communication," in *Handbook of Squirrel Monkey Research*, edited by L. A. Rosenblum and C. L. Coe (Plenum, New York), pp. 99–126.
- Newman, J. D. (1985b). "The infant cry of primates: An evolutionary perspective," in *Infant Crying: Theoretical and Research Perspectives*, edited by B. M. Lester and C. F. Z. Boukydis (Plenum, New York), pp. 307–323.
- Newman, J. D., and Wollberg, Z. (1973a). "Responses of single neurons in the auditory cortex of squirrel monkeys to variants of a single call type," *Exp. Neurol.* **40**, 821–824.
- Newman, J. D., and Wollberg, Z. (1973b). "Multiple coding of species-specific vocalizations in the auditory cortex of squirrel monkeys," *Brain Res.* **54**, 287–304.
- Novick, A. (1977). "Acoustic Orientation," in *Biology of Bats, Vol. III*, edited by W. A. Wimsatt (Academic, New York), Chap. 2, pp. 74–287.
- Nowicki S., and Capranica, R. R. (1986). "Bilateral syringeal coupling during phonation of a songbird," *J. Neurosci.* **6**, 3595–3610.
- Payne, R. S., and McVay, S. (1971). Songs of humpback whales," *Science* **173**, 585–597.
- Petersen, M. R. (1982). "The perception of species-specific vocalizations by primates: A conceptual framework," in *Primate Communication*, edited by C. T. Snowdon, C. H. Brown, and M. R. Petersen (Cambridge U.P., Cambridge), pp. 171–211.
- Ploog, D., Hupfer, K., Jürgens, U., and Newman, J. D. (1975). "Neuroethological basis of vocalization in squirrel monkeys with special reference to genetic differences of calling in two subspecies," in *Growth and Development of the Brain*, edited by M. A. B. Brazier (Raven, New York), pp. 231–254.
- Pola, Y. V., and Snowdon C. T. (1975). "The vocalizations of pygmy marmosets (*Cebulla pygmaea*)," *Anim. Behav.* **26**, 192–206.
- Pollak, G. D., and Cassidy J. H. (1989). *The Neural Basis of Echolocation in Bats* (Springer-Verlag, Berlin).
- Porter, F. L. (1977). "Social behavior and acoustic communication in the bat, *Carollia perspicillata* (Chiroptera: phyllostomatidae)," Ph.D. dissertation, Washington Univ. pp. 100–115.
- Porter, F. L. (1979). "Social behavior in the leaf-nosed bat, *Carollia perspicillata* II. Social communication," *Z. Tierpsychol.* **50**, 1–8.
- Ratcliffe, L., and Weisman, R. (1992). "Pitch processing strategies in birds: a comparison of laboratory and field studies," in *Playback and Studies of Animal Communication*, edited by P. K. McGregor (Plenum, New York), pp. 211–224.
- Robinson, J. G. (1982). "Vocal systems regulating within-group spacing," in *Primate Communication*, edited by C. T. Snowdon, C. H. Brown, and M.

- R. Petersen (Cambridge U.P., Cambridge, England), pp. 94–116.
- Rowell, T. E., and Hinde, R. A. (1962). "Vocal communication by the rhesus monkey, (*Macaca mulatta*)," *Proc. Zool. Soc. London* **138**, 279–294.
- Sales, G., and Pye, D. (1974). *Ultrasonic Communication by Animals* (Chapman and Hall, London).
- Seyfarth, R. M., Cheney, D. L., and Marler, P. (1980). "Monkey responses to three different alarm calls: evidence of predator classification and semantic communication," *Science* **210**, 801–803.
- Snowdon, C. T. (1982). "Linguistic and pschyolinguistic approaches to primate communication," in *Primate Communication*, edited by C. T. Snowdon, C. H. Brown, and M. R. Petersen (Cambridge U.P., Cambridge, England), pp. 212–238.
- Snowdon, C. T., Brown, C. H., and Petersen, M. R. (1982). *Primate Communication* (Cambridge U.P., Cambridge, England).
- Struhsaker, T. (1976). *Behavior and Ecology of Red Colobus Monkeys* (University of Chicago, Chicago).
- Suga, N. (1971). "Analysis of information bearing elements in complex sounds by auditory neurons of bats," *Audiology* **11**, 58–72.
- Suga, N. (1978). "Specialization of the auditory system for reception and processing of species-specific sounds," *Fed. Proc.* **37**, 2342–2354.
- Suga, N. (1984). "The extent to which biosonar information is represented in the bat auditory cortex," in *Dynamic Aspects of Neocortical Function*, edited by G. M. Edelman, W. E. Gall, and W. M. Cowan (Wiley, New York), pp. 315–373.
- Suga, N. (1990). "Cortical computational maps for auditory imaging," *Neural Networks* **3**, 3–21.
- Suga, N. (1992). "Philosophy and Stimulus Design for neuroethology of complex sound processing," *Philos. Trans. R. Soc. London Ser. B* **336**, 423–428.
- Suthers, R. A. (1988). "The production of echolocation signals by bats and birds," in *Animal Sonar. Processes and Performance*, edited by P. E. Nachtigall and P. W. B. Moore (Plenum, New York), pp. 23–45.
- Suthers, R. A., and Fattu, J. M. (1973). "Mechanisms of sound production by echolocating bats," *Am. Zool.* **13**, 1215–1226.
- Sutton, D. (1979). "Mechanisms underlying vocal control in nonhuman primates," in *Neurobiology of Social Communication in Primates: An Evolutionary Perspective*, edited by H. D. Steklis and M. J. Raleigh (Academic, New York), pp. 45–65.
- Thomas, W. T., Fenton, M. B., and Barclay, R. M. R. (1979). "Social behavior of the little brown bat, *Myotis lucifugus* I. Mating behavior," *Behav. Ecol. Sociobiol.* **6**, 129–136.
- Wells, K. D., and Schwartz, W. J. (1984). "Vocal communication in a neotropical treefrog, *Hyla ebraccata*: advertisement calls," *Anim. Behav.* **32**, 405–420.
- Wilkinson, L. (1990). *SYSTAT: The System for Statistics* (SYSTAT, Inc., Evanston, IL), pp. 91–111.
- Williams, J. S. (1978). "A definition for the common-factor analysis model and the elimination of problems of factor score indeterminacy," *Psychometrika* **43**, 293.
- Winter, P., and Funkenstein, H. H. (1973). "The effect of species-specific vocalizations on the discharge of auditory cortical cells in the awake squirrel monkey," *Exp. Brain Res.* **18**, 489–504.
- Winter, P., Ploog, D., and Latta, J. (1966). "Vocal repertoire of the squirrel monkey (*Samiri sciureus*)," *Exp. Brain Res.* **18**, 489–504.
- Wollberg, Z., and Newman, J. D. (1972). "Auditory cortex of squirrel monkey: Response patterns of single cells to species-specific vocalizations," *Science* **175**, 212–214.